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Osteology and Morphology of Fishes of the Subfamily Salariinae and its Junior Synonym Parablenniinae (Pisces: Blenniidae)

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With 34 figures and 3 tables

Summary

Osteological and morphological characters of the subfamilies Parablenniinae Miranda-Ribeiro, 1915 and Salariinae Cuvier, 1817 (former tribes Parablenniini and Salariini) are examined. Not a single feature is found that is characteristic for either group. The pattern of dentition (incisiform or comblike teeth) which was previously used to distinguish the two tribes is not constant. Several intermediate forms between incisiform and comblike teeth exist, independent of phylogenetic relationships. An evolutionary trend to form a comblike dentition out of an incisiform dentition is observed.

Based on these results, the two tribes are synonymized with the older subfamily name Salariinae (type genus *Salarias* Cuvier, 1817) as the senior synonym.

Zusammenfassung

Die osteologischen und morphologischen Merkmale der Fische der Unterfamilien Parablenniinae Miranda-Ribeiro, 1915 und Salariinae Cuvier, 1817 (bisherige Tribus Parablenniini und Salariini) werden untersucht. Dabei kann kein Merkmal gefunden werden, das nur bei einer dieser beiden Gruppen nachweisbar ist. Die Art der Bezahnung (Schneidezahn- oder Kammzahngebiss), die bisher als wichtigstes Unterscheidungsmerkmal für diese beiden Gruppen angesehen wurde, ist für keine der beiden ein konstantes Unterscheidungsmerkmal. Zwischen Schneidezahn- und Kammerzahngebiss finden sich (unabhängig von direkten verwandtschaftlichen Beziehungen) zahlreiche Übergangsformen, wobei offensichtlich eine Tendenz zur Ausbildung eines Kammzahngebisses aus einem Schneidezahngebiss besteht.

Aufgrund dieser Befunde werden beide Gruppen in der älteren Unterfamilie Salariinae (mit der Typusgattung *Salarias* Cuvier, 1817) zusammengefasst.

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1. Introduction

NORMAN (1943) was the first to publish an infrafamilial classification of the Blenniidae including a synopsis of blenniid fish genera. Species of the family Blenniidae were grouped in three subfamilies, mainly on the basis of different types of dentition: Ophioblenniinae, Blenniinae, and Salariinae.

Later authors modified NORMAN's classification into present usage. The main works were published by SPRINGER (1967, 1968, 1972, 1988), SMITH-VANIZ & SPRINGER (1971), SPRINGER & SMITH-VANIZ (1972), SMITH-VANIZ (1975, 1976), SPRINGER & GOMON (1975), BATH (1977, 1982, 1983, 1989, 1990, 1992), WILLIAMS (1988, 1990), BATH & WIRTH (1989, 1992) and SPRINGER & WILLIAMS (1994). On the basis of osteological characters, SPRINGER (1968) distinguished within the family Blenniidae a subfamily Blenniinae with the three tribes Blenniini, Omobranchini and Salariini, and another subfamily Nemophidinae.

In his characterization of the tribe Blenniini, SPRINGER (1968: 47) pointed out that only the two species *Blennius ocellaris* Linnaeus, 1758 and *B. normani* Poll, 1949 have dentaries connected by a serrate suture, not by a fibrose syndesmosis. He also found that in these two species the distal end of the ascending premaxillary process is widely attached to the base of the median ethmoid, while all other species of the Blenniini have a premaxillary process situated before the median ethmoid. SPRINGER suggested that the tribe Blenniini (except for *Blennius ocellaris* and *B. normani*) might be the least specialized tribe in the family Blenniidae. The tribe Omobanchiini probably originated from a Blenniini-like ancestor; *Blennius ocellaris* and *B. normani* were probably intermediate between the tribe Omobranchiini and other »Blenniini« (SPRINGER, 1968: 50–51).

SPRINGER also proposed that the tribe Salariini originated from a Blenniini-like ancestor. He characterized the Salariini as possessing a combtooth dentition with the teeth being only loosely attached to the premaxillary and the dentary by a thick band of connective tissue.

SMITH-VANIZ & SPRINGER (1971) gave a synopsis of the tribe Salariini, and again defined the characters in detail. In genera of this tribe that posses a typical combtooth dentition, the numerous teeth on the premaxillary and dentary are not formed within these bones; the bases of these teeth are not firmly connected with the premaxillary and dentary plates. The replacement teeth do not pass outward through special foramina.

Species of the genera *Alloblennius* Smith-Vaniz & Springer, *Antennablennius* Fowler, *Hirculops* Smith, *Litobranchus* Smith-Vaniz & Springer, *Medusablennius* Springer, *Mimoblennius* Smith-Vaniz & Springer and *Rhabdoblennius* Whitley have a dentition intermediate between the tribes Blenniini and Salariini; SMITH-VANIZ & SPRINGER (1971) assigned them to the tribe Salariini.

SPRINGER & SMITH-VANIZ (1972) erected another tribe, Phenablenniini, represented by the monotypic genus *Phenablennius* Springer & Smith-Vaniz, with *Phena-*

blennius heyligeri (Bleeker, 1859) as the only species. In the same paper (SPRINGER & SMITH-VANIZ, 1972: 64), the subfamily Nemophidinae was degraded into a tribe Nemophini without comment; it was later revised as tribe Nemophini by SMITH-VANIZ (1976). In the latter revision, SMITH-VANIZ made a detailed examination of the phylogenetic position of the Nemophini within the family Blenniidae (on the basis of SPRINGER, 1968 and SPRINGER & SMITH-VANIZ, 1972); considering plesiomorphic and apomorphic characters, he recognized 6 major lineages within the family Blenniidae (SMITH-VANIZ, 1976: fig. 88): Tribe Salariini; »Blenniini«-group; species of genus *Blennius;* Tribe Omobranchini; Tribe Phenablenniini; Tribe Nemophini.

BOCK & ZANDER (1986) included the genera of the »Blenniini«-group in a new tribe Parablenniini, which they proposed was the sister-tribe of the Salariini. On the other hand, they distinguished the tribes Blenniini (containing species of the genus *Blennius*), Omobranchini, Phenablenniini and Nemophini, thus adding to 6 tribes within the family Blenniidae.

BATH & WIRTZ (1989) added another genus, *Spaniblennius* (with two species) to the tribe Blenniini. They summarized the characters which are typical for the tribe Blenniini.

WILLIAMS (1990) again examined the phylogeny of the tribes of blenniid fishes; he hypothesized a close relationship between the tribes Parablenniini and Salariini. The monophyly of the Parablenniini was based on two synapomorphies, configuration of basibranchial I and epibranchial IV (WILLIAMS, 1990: 8). He hypothesized the monophyly of the Salariini based on the configuration of the premaxillary and the shape of the infrapharyngobranchial plate. In a preliminary hypothesis of the blenniid tribe relationships, he divided the Salariini into two groups, a *Rhabdoblennius*-group with an atypical dentition, and a *Salarias*-group with a typical dentition (WILLIAMS, 1990: fig. 1).

2. Methods, materials and acknowledgments

2.1. Methods

Measurements were made with a dial caliper to the nearest 0.1 mm. Standard length *(SL)* was measured from the mid-tip of the upper lip to the distal end of the urostyle; total length *(TL)* was measured from the mid-tip of the upper lip to the tip of the longest caudal fin ray.

All specimens were treated with the trypsin-alizarin method of TAYLOR (1967). On the basis of cleared-and-stained specimens, additional preparations were made.

Photographs were taken with a ZEISS binocular SR, a photo tube and a LEICA R 4 camera, using AGFAPAN AP x 25 films.

The osteological nomenclature is based on SPRINGER (1968) and other blenniid osteological literature. The following abbreviations are used in the figure captions:

ACT Anterior canine tooth;
AID anterior-inferior margin of the dentary;
ASP anterior-superior margin of the premaxillary;
BB bone bridge;
BP bony particle;
BR rodlet-like bony particle;
CP premaxillary cavity *(cavum praemaxillare);*
CT comblike teeth;
CTI connective tissue;
CTO canine tooth;
DE dentary;

DPF dental plate of functional teeth;
DT dentine;
ET dental enamel;
FO foramen through which replacement teeth grow outward;
FRON frontal;
FT functinal teeth;
IT incisiform teeth;
KIN kinethmoid;
LAETH lateral ethmoid;
MAX maxillary;
METH median ethmoid;
NAS nasal;
PAL palatine;
PCT posterior canine tooth;
PD dental protuberance;
PIP posterior-inferior margin of the premaxillary;
PM premaxillary;
PMP mandibular part of opercular canal;
PPS ascending process of premaxillary;
PSD posterior-superior margin of dentary;
RT replacement teeth;
TR tooth ridge;
a anterior;
c caudal;
i inferior;
l lateral;
le left;
m medial;
p posterior;
r rostral;
ri right;
s superior.

In addition to blenniids, the carangid *Hemicaranx leucurus* was examined as an outgroup; that species possesses a complete number of radials on the scapula of the shoulder girdle which represents the plesiomorphic condition.

The following nominal genera in the subfamilies Parablenniinae and Salariinae (former tribes Parablenniini and Salariini) are recognized:

Subfamily Parablenniinae

Aidablennius Whitley, 1947 (type species: *Blennius sphynx* Valenciennes in Cuvier & Valenciennes, 1836 by original designation and monotypy);
Bathyblennius Bath, 1977 (type species: *Blennius antholops* Springer & Smith-Vaniz, 1970 by original designation and monotypy);
Chalaroderma Norman, 1943 (type species: *Blennius capito* Valenciennes in Cuvier & Valenciennes, 1836 by original designation and monotypy);
Chasmodes Valenciennes in Cuvier & Valenciennes, 1836 (type species: *Blennius bosquianus* Lacepède, 1800 by subsequent designation of JORDAN & EVERMANN, 1898: 2391);
Coryphoblennius Norman, 1943 (type species: *Blennius galerita* Linnaeus, 1758 by original designation and monotypy);
Hypleurochilus Gill, 1861 (type species: *Blennius multifilis* Girard, 1858 by subsequent designation of GILL, 1861: 168);
Hypsoblennius Gill, 1861 (type species: *Blennius hentzi* LeSueur, 1825 by monotypy);
Lipophrys Gill, 1896 (type species: *Blennius pholis* Linnaeus, 1758; replacement name for *Pholis* Cuvier, 1816, preoccupied by *Pholis* Scopoli, 1777);
Lupinoblennius Herre, 1942 (type species: *Lupinoblennius dispar* Herre, 1942 by original designation and monotypy);

Parablennius Miranda-Ribeiro, 1915 (type species: *Blennius pilicornis* Valenciennes in Cuvier & Valenciennes, 1836 by monotypy);
Parahypsos Bath, 1982 (type species: *Hypsoblennius piersoni* Gilbert & Starks, 1904; replacement name for *Leptoblennius* Bath, 1978, preoccupied by *Leptoblennius* Gill, 1860);
Salaria Forsskål, 1775 (type species: *Blennius basiliscus* Valenciennes in Cuvier & Valenciennes, 1836 by subsequent designation by JORDAN & EVERMAN, 1898: 2377);
Scartella Jordan, 1886 (type species: *Blennius microstomus* Poey, 1861 by original designation and monotypy).

Subfamily Salariinae

Alloblennius Smith-Vaniz & Springer, 1971 (type species: *Rhabdoblennius pictus* Lotan, 1970 by original designation);
Alticus Commerson in Lacepède, 1800 (type species: *Blennius saliens* Lacepède, 1800);
Andamia Blyth, 1858 (type species: *Andamia expansa* Blyth, 1858 by monotypy);
Antennablennius Fowler, 1931 (type species: *Blennius hypenetes* Klunzinger, 1871 by original designation and monotypy);
Atrosalarias Whitley, 1933 (type species: *Salarias phaiosoma* Bleeker, 1855 by original designation);
Blenniella Reid, 1943 (type species: *Blenniella rhessodon* Reid, 1943 by original designation and monotypy);
Cirripectes Swainson, 1839 (type species: *Salarias variolosus* Valenciennes in Cuvier & Valenciennes, 1836 by monotypy);
Cirrisalarias Springer, 1976 (type species: *Cirrisalarias bunares* Springer, 1976 by original designation and monotypy);
Crossosalarias Smith-Vaniz & Springer, 1971 (type species: *Crossosalarias macrospilus* Smith-Vaniz & Springer, 1971 by original designation and monotypy);
Dodekablennos Springer & Spreitzer, 1978 (type species: *Dodekablennos fraseri* Springer & Spreitzer, 1978 by original designation and monotypy);
Ecsenius McCulloch, 1923 (type species: *Ecsenius mandibularis* McCulloch, 1923 by original designation and monotypy);
Entomacrodus Gill, 1859 (type species: *Entomacrodus nigricans* Gill, 1859 by monotypy);
Exallias Jordan & Evermann, 1905 (type species: *Salarias brevis* Kner, 1868 by original designation and monotypy);
Glyptoparus Smith, 1959 (type species: *Glyptoparus delicatulus* Smith, 1959 by original designation);
Hirculops Smith, 1959 (type species: *Blennius cornifer* Rüppell, 1828 by original designation and monotypy);
Istiblennius Whitley, 1943 (type species: *Salarias muelleri* Klunzinger, 1879 by original designation and monotypy);
Litobranchus Smith-Vaniz & Springer, 1971 (type species: *Salarias fowleri* Herre, 1926 by original designation and monotypy);
Medusablennius Springer, 1966 (type species: *Medusablennius chani* Springer, 1966 by original designation and monotypy);
Mimoblennius Smith-Vaniz & Springer, 1971 (type species: *Blennius atrocinctus* Regan, 1909 by original designation);
Nannosalarias Smith-Vaniz & Springer, 1971 (type species: *Blennius nativitatis* Regan, 1909 by original designation and monotypy);
Ophioblennius Gill, 1860 (type species: *Blennophis webbii* Valenciennes in Webb & Berthelot, 1843; replacement name for *Blennophis* Valenciennes, 1843, preoccupied by *Blennophis* Swainson, 1839);
Paralticus Springer & Williams, 1994 (type species: *Salarias amboinensis* Bleeker, 1857 by original designation and monotypy);
Pereulixia Smith, 1959 (type species: *Salarias kosiensis* Regan, 1908 by original designation and monotypy);
Praealticus Schultz & Chapman in Schultz et alii, 1960 (type species: *Salarias natalis* Regan, 1909 by original designation);

Rhabdoblennius Whitley, 1930 (type species: *Blennius rhabdotrachelus* Fowler & Ball, 1924 by original designation);
Salarias Cuvier, 1816 (type species: *Salarias quadripennis* Cuvier, 1816 by subsequent designation of JORDAN, 1917: 101);
Scartichthys Jordan & Evermann, 1898 (type species: *Salarias rubropunctatus* Valenciennes in Cuvier & Valenciennes, 1836; replacement name for *Scartes* Jordan & Evermann, 1896, preoccupied by *Scartes* Swainson, 1835 in Mammalia);
Stanulus Smith, 1959 (type species: *Stanulus seychellensis* Smith, 1959 by original designation and monotypy).

2.2. Materials

For the osteological examination, the specimens listed below were examined (families, genera and species in alphabetical order; standard length is given in mm). Specimens used for counts and measurements are not listed separately. The following acronyms are used in the text:

NMW Naturhistorisches Museum, Wien, Austria;
SB Sammlung BATH, Pirmasens, Germany;
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany;
USNM National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.;
WAM Western Australian Museum, Perth, Australia.

Material for osteological examination:

Family Blenniidae

Aidablennius sphynx (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 male, 53.0 mm SL; Marmara Sea, Turkey, Erdek, near Bandirma.
Alloblennius pictus (Lotan, 1969): SB uncat., 1 female, 21.3 mm SL; Red Sea, Egypt, Sinai, Sharm-el-Sheijkh.
Alticus andersonii (Day, 1876): SB uncat., 1 male, 66.3 mm SL; Indian Ocean, Sri Lanka, Trincomalee.
Antennablennius adenensis Fraser-Brunner, 1951: SB uncat., 1 male, 38.5 mm SL; Red Sea, Eritrea, Dahlak Archipelago, Romia Island; coll. L. FISHELSON.
Antennablennius australis Fraser-Brunner, 1951: SB uncat., 1 male, 38.5 mm SL; Red Sea, Eritrea, Dahlak Archipelago, Romia Island; coll. L. FISHELSON.
Antennablennius ceylonensis Bath, 1983: SB uncat., 1 male, 39.6 mm SL; Indian Ocean, Sri Lanka, Trincomalee, Sweat Bay.
Antennablennius hypenetes (Klunzinger, 1871): SB uncat., 1 male, 49.8 mm SL; Indian Ocean, Gulf of Aden, Seba Island.
Blenniella cyanostigma (Bleeker, 1849): SB uncat., 1 male, 50.7 mm SL; Indian Ocean, Sri Lanka, Galle.
Chasmodes saburrae Jordan & Gilbert, 1882: SB uncat., 1 male, 52.0 mm SL; Gulf of Mexico, U.S.A., Florida, Levy County, Rum Key.
Cirripectes castaneus (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 male, 23.6 mm SL; Red Sea, Egypt, Sinai, Naama Bay.
Cirripectes vanderbilti (Fowler, 1938): SB uncat., 1 male, 69.8 mm SL; Pacific Ocean, U.S.A., Johnston Island.
Cirrisalarias bunares Springer, 1976: USNM 339746, 1 female, 24.0 mm SL; Indian Ocean, Mauritius, west coast, Albion.
Coryphoblennius galerita (Linnaeus, 1758): SB uncat., 2 females, 46.4–49.6 mm SL; Mediterranean Sea, Spain, Taramay, W of Motril. – SB uncat., 1 male, 61.5 mm SL; Mediterranean Sea, Spain, Torremolinos. – SB uncat., 1 female, 57.0 mm SL; Mediterranean Sea, Italy, Sicily, Isola delle Femine, E of Palermo.
Dodekablennos fraseri Springer & Spreitzer, 1978: USNM 344273, 1 female, 29.3 mm SL; Indian Ocean, Mauritius, south coast, Bel Air.
Ecsenius bicolor (Tickell & Day in Day, 1888): SB uncat., 1 male, 47.0 mm SL; Indian Ocean, Indonesia, Bali, Padang Bay; coll. R. A. PATZNER.

Enchelyurus petersi (Kossman & Räuber, 1877): USNM 204540, 1 male, 50.0 mm SL; Gulf of Aden.
Entomacrodus cadenati Springer, 1966: SB uncat., 1 male, 53.2 mm SL; East Atlantic Ocean, Senegal, Dakar, Ile de Gorée.
Entomacrodus vermiculatus (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 female, 84.3 mm SL; Indian Ocean, Sri Lanka, Trincomalee.
Exallias brevis (Kner, 1868): SB uncat., 1 male, 77.8 mm SL; Pacific Ocean, Taiwan, Lanyu; coll. S.-C. Lee.
Hirculops cornifer (Rüppell, 1830): SB uncat., 1 male, 48.4 mm SL; Red Sea, Egypt, Sinai, Ras Burka; coll. L. Fishelson.
Hypleurochilus bananensis (Poll, 1959): SB uncat., 1 female, 52.5 mm SL; Mediterranean Sea, Algeria, Algier, port.
Hypsoblennius brevipinnis (Günther, 1861): USNM 322803, 1 male, 27.7 mm SL; East Pacific Ocean, Panama, Peninsula de Azuero.
Hypsoblennius gilberti (Jordan, 1882): SB uncat., 1 male, 74.5 mm SL; East Pacific Ocean, U.S.A., California, Los Angeles, Palos Verdes.
Hypsoblennius paytensis Steindachner, 1876: NMW 47484, 1 male, 85.0 mm SL; East Pacific Ocean, Peru, Paita.
Hypsoblennius striatus Steindachner, 1876: SB uncat., 1 male, 59.0 mm SL; East Pacific Ocean, Panama; coll. C. E. Dawson.
Istiblennius edentulus (Schneider & Forster in Bloch & Schneider, 1801): SB uncat., 1 female, 74.4 mm SL; Indian Ocean, Sri Lanka, Hikkaduwah.
Istiblennius lineatus (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 male, 83.0 mm SL; Indian Ocean, Sri Lanka, Bentota.
Istiblennius rivulatus (Rüppell, 1830): SB uncat., 1 male, 96.5 mm SL; Red Sea, Gulf of Aqaba, Israel, Eilat.
Lipophrys canevae (Vinciguerra, 1880): SB uncat., 1 male, 60.0 mm SL; Mediterranean Sea, Greece, Gulf of Epidavros, Kyra Island.
Lipophrys dalmatinus (Seindachner & Kolombatovic, 1883): SB uncat., 1 male, 38.0 mm SL; Mediterranean Sea, Adriatic Sea, Croatia, Istria, Medulin.
Lupinoblennius vinctus (Poey, 1867): SB uncat., 1 male, 35.0 mm SL; Caribbean Sea, Panama, Bahia Limón; coll. C. E. Dawson.
Mimoblennius atrocinctus (Regan, 1909): SB uncat., 1 male, 33.6 mm SL; Indian Ocean, Sri Lanka, Trincomalee.
Nannosalarias nativitatis (Regan, 1909): SB uncat., 1 male, 28.2 mm SL; Indian Ocean, Australia, Christmas Island; coll. G. R. Allen.
Omobranchus punctatus (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 female, 37.0 mm SL; Indian Ocean, Sri Lanka, Trincomalee.
Parablennius goreensis (Valenciennes in Cuvier & Valenciennes, 1836: SB uncat., 1 female, 39.5 mm SL; East Atlantic Ocean, Senegal, Dakar Ile de Gorée.
Parablennius incognitus Bath, 1968: SB uncat., 1 male, 51.8 mm SL; Mediterranean Sea, Adriatic Sea, Croatia, Istria, Medulin.
Parablennius pilicornis (Cuvier, 1829): SB uncat., 1 male, 84.0 mm SL; Mediterranean Sea, Spain, Taramay, W of Motril. – SB uncat., 1 female, 75.8 mm SL; Northeast Atlantic Ocean, France, Bay of Biscay, Côte des Basques, Hendaye.
Parablennius tentacularis (Brünnich, 1768): SB uncat., 1 female, 65.8 mm SL; Mediterranean Sea, Croatia, Biograd na Moru, 20 km ESE Zadar.
Paralipophrys trigloides (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 female, 73.5 mm SL; Mediterranean Sea, Italy, Sicily Island, Castellamare.
Plagiotremus azaleus (Jordan & Bollman, 1890): USNM 200932, 1 male, 45.3 mm SL; East Pacific Ocean, Mexico, Baja California Sur.
Praealticus poptae (Fowler, 1925): SB uncat., 1 male, 48.1 mm SL; Pacific Ocean, Commonwealth of the Northern Marianas, Agrihan Island.
Praealticus tanegasimae (Jordan & Starks, 1906): SB uncat., 1 male, 87.6 mm SL; Pacific Ocean, Japan, Tanega-shima, Nishi-no-Omote.
Rhabdoblennius ellipes (Jordan & Starks, 1906): SB uncat., 1 female, 50.4 mm SL; Pacific Ocean, Taiwan, Lu-tao.

Salarias fasciatus (Bloch, 1786): SB uncat., 1 male, 41.0 mm SL; Indian Ocean, Sri Lanka, Galle.
Salarias sinuosus Snyder, 1908: SB uncat., 1 male, 33.6 mm SL; Indian Ocean, Sri Lanka, Trincomalee, Fort Frederick.
Scartella cristata (Linnaeus, 1758): SB uncat., 1 male, 93.5 mm SL; East Atlantic Ocean, Angola.

Family Carangidae

Hemicaranx leucurus (Günther, 1864): USNM 82190, 1 specimen, 36.7 mm SL; East Pacific Ocean, Panama, Punta Chame.

2.3. Acknowledgments

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3. Dentition of the Parablenniinae and Salariinae

A detailed osteological examination of the dentition and additional important characters of species of the Parablenniinae and Salariinae (former tribes Parablenniini Miranda-Ribeiro, 1915 and Salariini Cuvier, 1817) results in a new classification. Several intermediate forms are found between species and genera with an incisiform dentition on the one hand and a combtooth dentition on the other. These intermediate species and genera have hitherto been assigned to the tribe Salariini (Springer, 1968; Smith-Vaniz & Springer, 1971).

In the present paper, the genera of the former tribes Parablenniini and Salariini are classified in four different groups, characterized as follows:

Group 1: Genera with an incisiform dentition
Premaxillary and dentary form a closed bony capsule. Inferior margin of the premaxillary and superior margin of the dentary with a tooth ridge that is firmly connected with the bases of the functional teeth. The replacement teeth are formed within the bony capsule exit through small foramina anterior to the bases of the functional teeth.
Members: Genera of the group Parablenniini except for the genus *Coryphoblennius.*

Group 2: Genera with a dentition intermediate between comblike and incisiform
a) The premaxillary and dentary tooth foramina vary in size; sometimes the bony bridges between the foramina are lost.
Members: Genera *Cirrisalarias, Coryphoblennius.*
b) Premaxillaries with a free anterior-superior median margin; laterally with replacement tooth foramina of different sizes. The dentaries form a close bony capsule with replacement tooth foramina of different sizes.
Member: Genus *Hirculops.*
c) Premaxillaries consisting of an incomplete bony capsule without a closed bony cavity. Anterior-superior margins of premaxillary protruding freely. Functional teeth directly situated on the posterior-inferior premaxillary margin. Dentaries consisting of a closed bony capsule. Functional teeth of the dentaries situated dorsally on a tooth ridge. Replacement tooth foramina situated anterior on the base of the functional teeth.
Members: Genera *Antennablennius, Mimoblennius, Rhabdoblennius.*

Group 3: Genera with incomplete premaxillary and dentary capsules.
In both jaws, the dentition is intermediate between comblike and incisiform.
a) Anterior-superior margin of premaxillary and anterior-inferior margin of dentary freely protruding. All functional teeth connected with the posterior-inferior margin of the premaxillary and with the posterior-superior margin of the dentary.
Members: Genera *Nannosalarias, Dodekablennos.*
b) Bases of lateral functional premaxillary teeth not connected with posterior-inferior margin of premaxillary, but extending beyond the lateral margin of the bone. Bases of functional dentary teeth connected with the posterior-superior margin of the dentary.
Member: *Ecsenius bicolor.*

Group 4: Genera possessing open premaxillary and dentary capsules with an inferior excavation of the premaxillary and a superior excavation of the dentary (Springer, 1968; Smith-Vaniz & Springer, 1971).
The functional teeth are not in direct contact with the jaw bones. The bases of the functional teeth are connected to the posterior-inferior margin of the premaxillary and the posterior-superior margin of the dentary by tight membranous tissue with bony inlays.
Members: *Alticus andersonii, Blenniella cyanostigma, Entomacrodus vermiculatus, Exallias brevis, Istiblennius edentulus, I. linatus, I. rivulatus, Praealticus poptae, P. tanegasimae, Salarias fasciatus, S. sinuosus.*

Premaxillaries and dentaries are called an incomplete bony capsule if the anterior-superior or the anterior-inferior margin is protruding freely, and if the posterior-inferior or the posterior-superior margin is connected with the functional teeth. The bony capsule is complete if the jaw margin and the functional teeth are not in direct contact (Fig. 1).

In the present paper, some species and genera of the former Parablenniinae and Salariinae could not be examined. Future studies are needed to determine their dentition types. It is possible that additional types of dentition may be found.

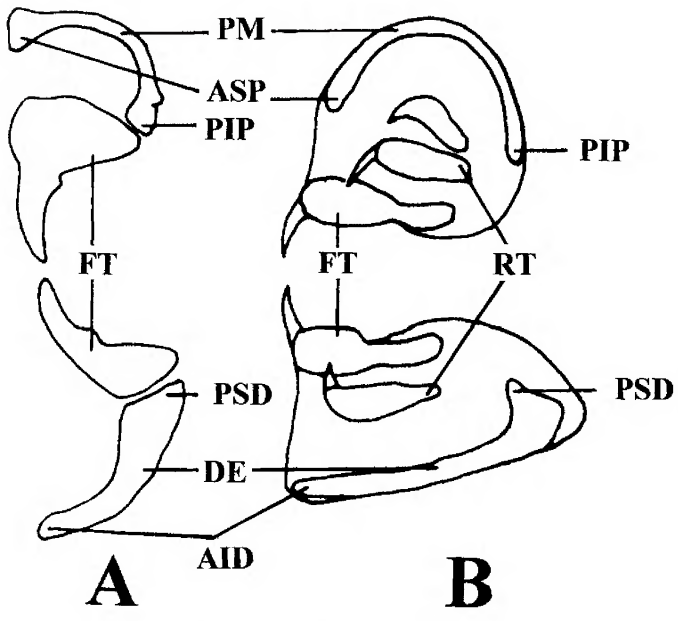


Fig. 1. Median sides ob blenniid premaxillaries and dentaries (schematic). – *A* incomplete shell-like shape; – *B* complete shell. – *Abbreviations:* see chapter 2.1.

4. Morphology of functional teeth

The teeth mainly consist of dentine and dental enamel. The dentine solidifies and supports the tooth; it is found towards the base of the tooth. As the dentine is very similar to bony tissue, it is easily stained with alizarin. The unstained dental cement forms the distal parts of the tooth (Fig. 2 A: 4, 7–8); it is either situated within the dentine (Fig. 2 A: 1–2, 6), or completely encloses the tooth (Fig. 2 A: 1, 3, 5, 9–10). The dentine may be quadrangular-shaped (Fig. 2 B: 5, 10), may extend towards the tip of the tooth (Fig. 2 A: 1–3, 6, 11), or may form a network structure extending from the base towards the tip (Fig. 2 A: 1).

During the evolution of the dentition from the more primitive incisiform to the more advanced comblike type, the tooth configuration likewise changes, so that it is usually characteristic for the type of dentition.

Teeth of the incisiform type are usually found in species with a low tooth number that are more or less carnivorous. Incisors, which are firmly connected to the tooth ridges, have a broad base in a longitudinal direction. They are stout, usually with a strong tip. Their posterior side is often supported by a bony protuberance *(protuberantia dentalis)*, that is most characteristic in typical incisors or teeth intermediate between the incisiform and the comblike types (Fig. 2 A–B; 1, 3, 5, 7).

Exallias brevis has most remarkable teeth; they are quite numerous in the upper jaw, numbering from 194–210 (SMITH-VANIZ & SPRINGER, 1971), and are of a comblike type, while in the lower jaw they number from 52–62 and have an incisiform type (Fig. 2 A–B: 4). A similar dentition is found in the jaws of *Ecsenius bicolor*, with 112 upper jaw teeth and 34 lower jaw teeth (Fig. 2 A–B: 6).

When the feeding habits gradually change into scraping and rasping to graze on the surface substrate, and a combtooth dentition is developed, the functional teeth become much more numerous. Typical comblike teeth are narrow and closely set. The tooth base is narrow, the distal tip of the tooth is angular and hooked (Fig. 2 A–B: 8–9, 11). For example, *Istiblennius rivulatus* has a typical comblike dentition (Fig. 2 A–B: 11) with more than 200 teeth each in the upper and lower jaws.

Canine teeth are usually found in the hind corners of the premaxillaries and dentaries. They are situated laterally, slightly behind the incisiform or comblike teeth. Canine teeth have a rounded base that is usually firmly connected with the jaw bone. In *Ecsenius,* besides the posterior canines an additional pair of anterior canines is present, directly following the lateral row of functional teeth.

As far as species of the former tribe Parablenniini have canine teeth, they are median sized in the upper jaw but large in the lower jaw. A total of 50 species has strong, posterior canine teeth in the premaxillaries and dentaries. In the two species *Parablennius gattorugine* and *P. ruber,* canine teeth may be present or absent in the upper jaw, but canine teeth in the lower jaw are always present. In the five known species of *Scartella,* canine teeth are generally absent from the upper jaw. In the genera *Chalaroderma* (2 species), *Chasmodes* (2 species), *Hypsoblennius* (14 species) and *Parahypsos* (1 species) canine teeth are always absent in both jaws (Tab. 1).

The size of canine teeth in the upper and lower jaws of the former tribes Parablenniini and Salariini is characterized as follows: Very small canine teeth do not reach the level of the tips of the functional teeth; small canine teeth reach level; medium sized canine teeth clearly exceed the level; large canine teeth may exceed the level more than twice the functional tooth length.

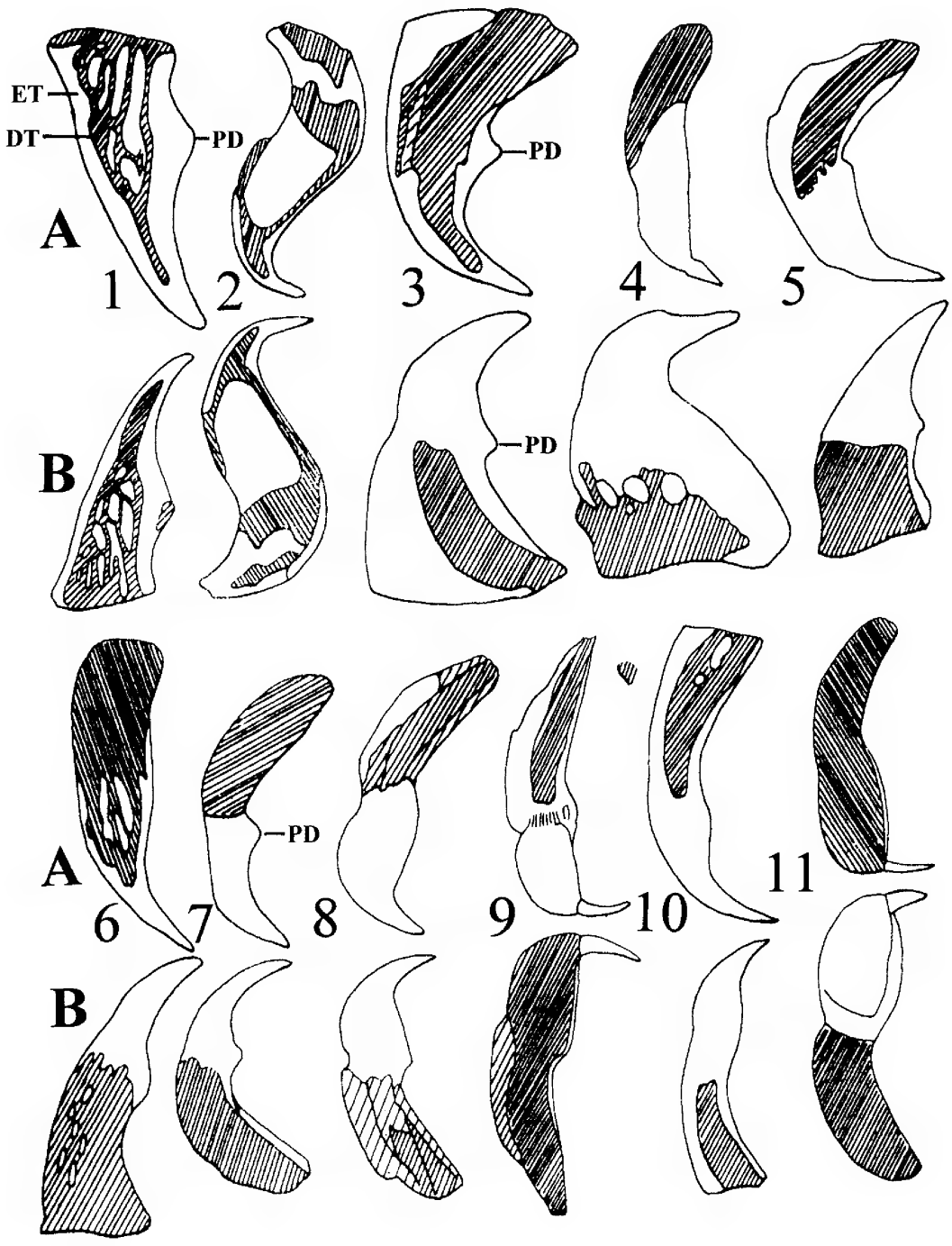


Fig. 2. Functional teeth in median sections of premaxillary *(A)* and dentary *(B)*. – 1. *Parablennius pilicornis*; – 2. *Coryphoblennius galerita*; – 3. *Antennablennius hypenetes*; – 4. *Exallias brevis*; – 5. *Mimoblennius atrocinctus*; – 6. *Ecsenius bicolor*; – 7. *Nannosalarias nativitatis*; – 8. *Blenniella cyanostigma*; – 9. *Entomacrodus vermiculatus*; – 10. *Salarias fasciatus*; – 11. *Istiblennius rivulatus*. – *Abbreviations: DT* dentine; *ET* dental enamel; *PD* dental protuberance.

Tab. 1. Numbers of incisiform teeth in upper and lower jaws of 13 genera of the Parablenniini. – *Explanations: U* Upper jaw; *L* lower jaw. Teeth present (+) or absent (–). Mean values in parentheses.

Genus/Number of specimens of species examined	Upper jaw teeth	Lower jaw teeth	Caniniform teeth	Vomerine teeth
Aidablennius (30 specimens)	31–36 (33.5)	29–33 (31.0)	U + L +	+
Lipophrys (8 species)	16–34 (19.2–24.9)	14–31 (17.9–22.9)	U + L +	– (3 spec.)
Parablennius (26 species)	19–40 (21.9–30.6)	16–39 (19.5–26.3)	U + L +	+ (17 spec.) – (9 spec.)
Paralipophrys (20 specimens)	20–33	16–27	U + L +	+
Salaria (3 species)	14–35 (24.0)	14–25 (19.0)	U + L +	+
Bathyblennius (holotype)	23	20	U + L +	–
Hypleurochilus (10 species)	18–36 (21.3–30.6)	19–36 (21.7–30.7)	U + L +	–
Scartella (5 species)	20–37 (25.4–33.8)	20–37 (22.0–30.8)	U – L +	–
Lupinoblennius (11 specimens)	20–25	16–20	U + L +/–	–
Chalaroderma (3 specimens)	26–37	25–38	U – L –	–
Chasmodes (4 specimens)	31–48	35–50	U – L –	–
Hypsoblennius (14 species)	20–44 (25.8–32.5)	24–47 (29.2–37.3)	U – L –	–
Parahypsos (5 specimens)	18–28	22–40	U – L –	–

Teeth of Group 1: Except for the genus *Coryphoblennius,* genera of the former group Parablenniinae have a typical incisiform dentition. Premaxillaries and dentaries form a completely closed bony capsule with a central bony cavity (premaxillary cavity and dentary cavity). In the sagittal plain, they are closely connected by a syndesmosis. On the ventral/dorsal side of the jaw bones a flat tooth ridge with longitudinal oval basal plates is found. The teeth are relatively firmly connected with

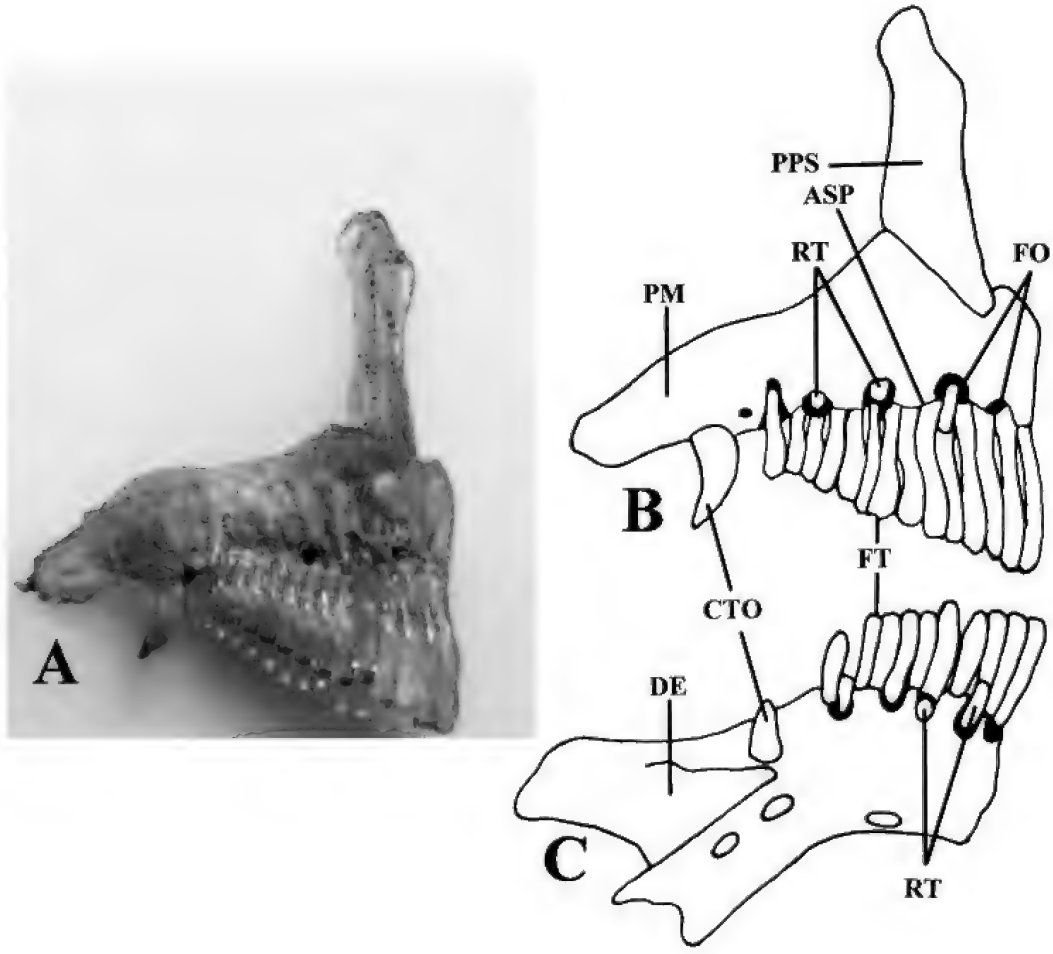
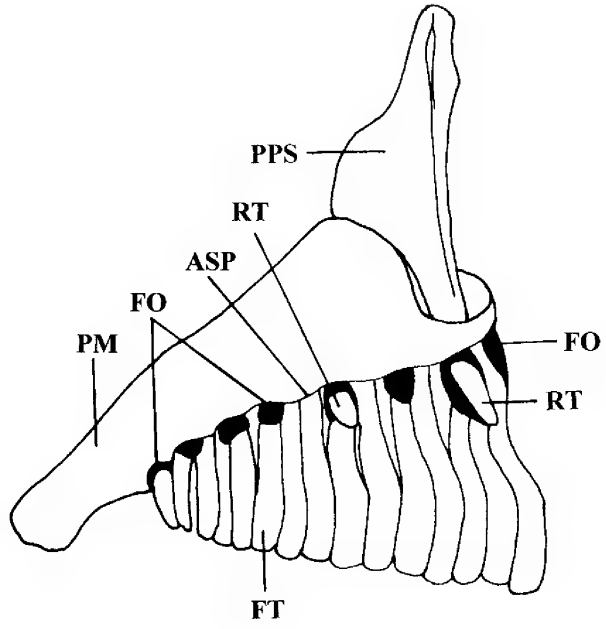


Fig. 3. *Parablennius pilicornis,* male, 84.0 mm SL. – *A.* Right premaxillary; – *B.* explanation of A; – *C.* right dentary.

these basal plates by a fibrous ankylosis. Premaxillaries and dentaries have small foramina which are situated directly before the bases of the functional teeth; through these foramina, the replacement teeth pass out of the jaw bones. The number of foramina is determined by the number of functional teeth. In the upper jaw, 14–48 functional teeth are found (usually less than 40 teeth); in the lower jaw, 14–50 (usually less than 40).

In many species, the number of functional teeth and replacement tooth foramina is increasing with growth. The number of premaxillary foramina varies from 8–16, that of the dentary foramina from 6–14.

Canine teeth in the premaxillary are absent in the genera *Chalaroderma, Chasmodes, Hypsoblennius, Parahypsos* and *Scartella,* usually also in *Parablennius gattorugine* (Fig. 4). Comparing the right-side premaxillaries of *Parablennius pilicornis* and *Scartella cristata* (Figs 3, 4), it is obvious that the anterior-superior margin of the premaxillary (which is not prominent) is situated above the replacement tooth foramina in *S. cristata;* also, one canine tooth is lacking in *S. cristata.* The number of foramina is higher in *S. cristata* than in *P. pilicornis,* though the number of functional



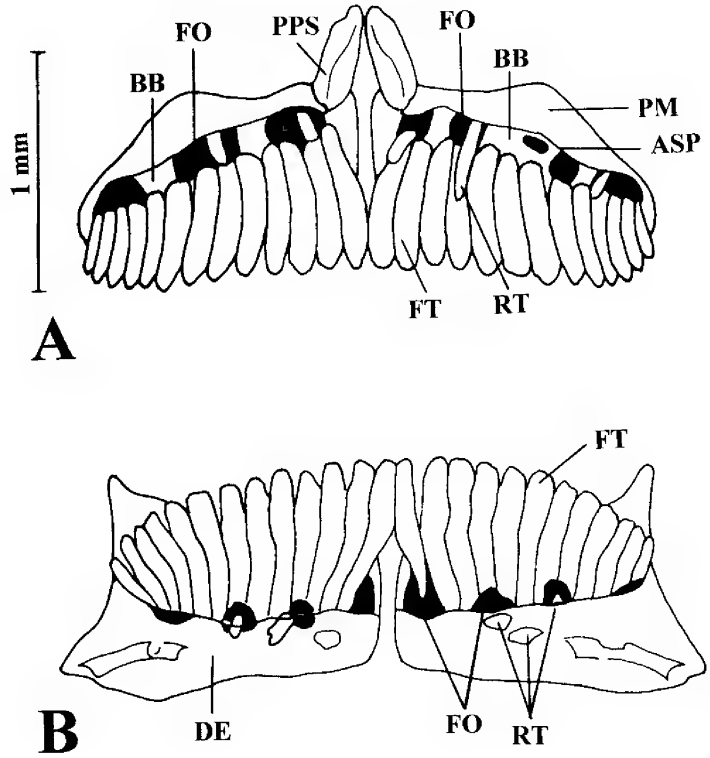


Fig. 4. *Scartella cristata,* male, 93.5 mm SL. – *(Upper):* Right premaxillary.
Fig. 5 *Cirisalarias bunares,* male, 24.0 mm SL. – *A.* Premaxillary, anterior side; – *B.* dentary, anterior side.

teeth is nearly equal, and the standard length of the two specimens in nearly identical. The dentition of *Scartella cristata* is very similar to that of *Cirrisalarias* (Fig. 5).

Teeth of Group 2: Species and genera of this group show a trend to change their feeding habits and thus to develop a comblike dentition from an incisiform type. The changes in different species occur independently in unrelated taxa. Some members of Group 2 have dentition patterns intermediate between the incisiform and comblike types, though there is a trend from the former to the latter that is more or less developed in different taxa of the group.

Cirrisalarias bunares has a freely protruding anterior-superior premaxillary margin, which is only connected with the posterior-inferior margin by few bony bridges of irregular widths between the replacement tooth foramina. The foramina are usually large, with different shapes (Fig. 5A). The functional teeth are barely mobile; they belong to the typical incisiform type. The number of functional teeth is low,

Tab. 2. Numbers of functional teeth in upper and lower jaws of 28 genera of the Salariini . – *Explanations: U* Upper jaw; *L* lower jaw. Teeth present (+) or absent (–). Mean values in parentheses. (Several values based on SMITH-VANIZ & SPRINGER, 1971.)

Genus/Number of specimens or species examined	Upper jaw teeth	Lower jaw teeth	Canini-form teeth	Vomerine teeth
Coryphoblennius	27–74	20–46	U – L +	+
Medusablennius	17–19	16–18	U – L –	–
Cirrisalarias	23–28	22–26	U – L –	–
Hirculops	34–44	22–26	U – L +	+
Antennablennius	31–42	21–34	U – L +/–	–
Alloblennius	34–38	30–36	U – L –	–
Litobranchus	40–42	23–30	U – L +	–
Mimoblennius	32–34	24–30	U – L +	–
Glyptoparus	74–80	50–58	U – L +	–
Nannosalarias	75–80	42–52	U – L +	+
Dodekablennos	55–63	44–47	U – L +	+
Crossosalarias	150	85–100	U – L +	–
Atrosalarias	185–226	120–147	U – L +	–
Salarias	110–168	72–134	U – L +	–
Ophioblennius	184–224	102–108	U – L +	–
Pereulixia	155–157	43–53	U – L +	+
Exallias	194–210	52–62	U – L –	–
Cirripectes	180–270	85–134	U – L +	–
Scartichthys	144–256	67–123	U – L +	–
Stanulus	118–138	62–82	U – L +	+/–
Entomacrodus	116–224	92–170	U – L +	+
Andamia	350–380	275–300	U – L –	–
Alticus	215–340	170–290	U – L +/–	+/–
Praealticus	130–300	96–214	U – L +/–	+/–
Blenniella	> 100	> 75	U – L +	–
Istiblennius	> 100	> 75	U – L +/–	–
Paralticus	> 100	> 75	U – L +/–	–
Ecsenius	> 95	13–62	U – L +[1)]	–

[1)] *Ecsenius* has 2 canini on each side of the lower jaw, the anterior attached to the incisiform teeth, the posterior free.

23–26 in the upper jaw, 22–26 in the lower jaw (SPRINGER, 1976). The teeth are attached to the posterior-inferior premaxillary margin. The dentaries form a closed bony capsule. The bases of the functional teeth are attached to a tooth ridge on the superior-median part of the dentary. The replacement tooth foramina are usually small (Fig. 5B). Canine and vomerine teeth are absent.

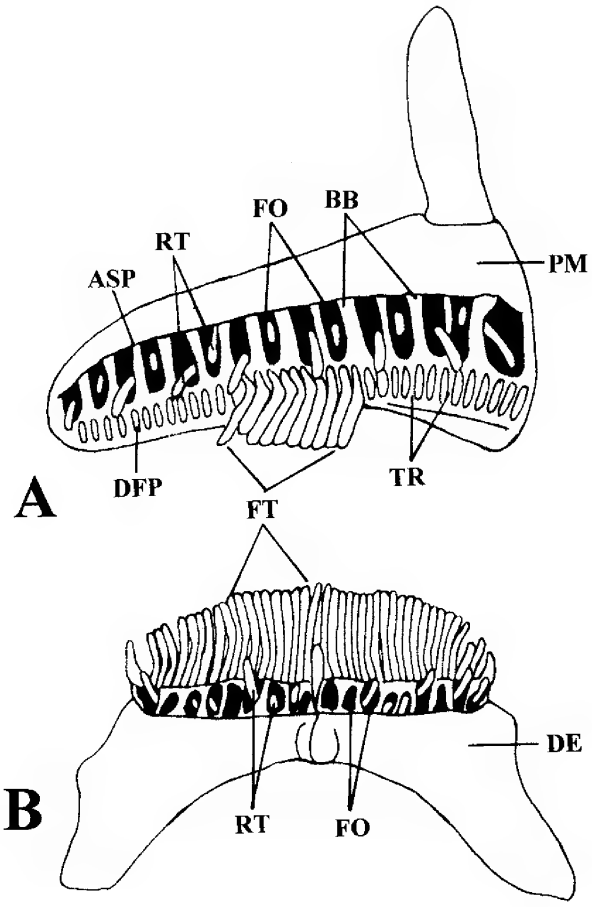
Coryphoblennius galerita was examined in detail by BATH (1994) and previously assigned to the tribe Parablenniini; it has another intermediate dentition pattern.

In Group 2, the number of premaxillary teeth may reach 74, and the dentary 46, which are higher numbers than in Group 1. The basal two-fifths of the functional teeth are bordered by papillae that extend as narrow branches in between the different teeth, and are continuous on the back side of the teeth as an epithelial layer. The replacement teeth are usually covered by these papillae.

The number of foramina which are situated in front of the base of the functional teeth is higher than in Group 1; their position is above the teeth bases, not closely before the bases. The foramina are much larger, and the bony bridges in between are much narrower. The superior end of these bony bridges is not on the same level with the frontal plate of the premaxillary, but situated behind; the premaxillary thus forms a sharp, continuous ridge that freely protudes anterior-inferiorly (Fig. 6A). The functional teeth are positioned on the tooth ridge of the posterior-inferior part of the premaxillary, and of the posterior-superior part of the dentary. The replacement teeth (when protruding from the jaw bone) are situated before the bases of the functional teeth (Fig. 7), not directly on the base as in Group 1.

The premaxillary of *Hirculops cornifer* forms an incompletely shell-like capsule with the midanterior two-fifths open. The anterior-inferior margin of this section ventrally protrudes roof-like (Fig. 8). The median functional teeth (teeth 9–11) are attached to a tooth ridge of the posterior-inferior margin of above mentioned shell; the lateral functional teeth are positioned on a tooth ridge of the lateral, closed section of the premaxillary. In the median section, replacement teeth freely grow below the anterior margin of the premaxillaries. In the lateral section, the replacement teeth pass out of foramina which are situated anterior to the functional teeth. The dentaries of *H. cornifer* are completely closed capsules. The functional dentary teeth are attached to a tooth ridge on the surface of the capsule. The replacement teeth are emitted through bony foramina (Fig. 8).

The jaws and dentition of four species of *Antennablennius (A. adenensis, A. australis, A. ceylonensis, A. hypenetes)* were examined. The premaxillary has a shell-like shape. The functional teeth are positioned on the basal plates of the tooth ridge on the posterior premaxillary margin (Fig. 9 A). The shape and connection with the tooth ridge is an unusual, special character of this genus. The premaxillary teeth are of the incisiform type, without any trace of a comb-like pattern. Two-fifths of the tooth base adjacent to the dentine are connected with the plates of the tooth ridge. Three-fifths of the tooth base (which consists of dental enamel) freely protrudes into the shall-like cavity. The anterior margin of the premaxillary shell is roof-like (Fig. 9 A). The median side of the premaxillaries is open, except for a narrow dorsal bony fringe (Fig. 10). The premaxillary replacement teeth are freely placed in the tooth-generating tissue; only when they become functional teeth do they contact the tooth ridge. The dentaries each form a closed capsule. All bases of the functional teeth are attached to the basal plates of a tooth ridge. The replacement teeth pass out of the bony cavity through usually 4 more or less narrow foramina which are situa-



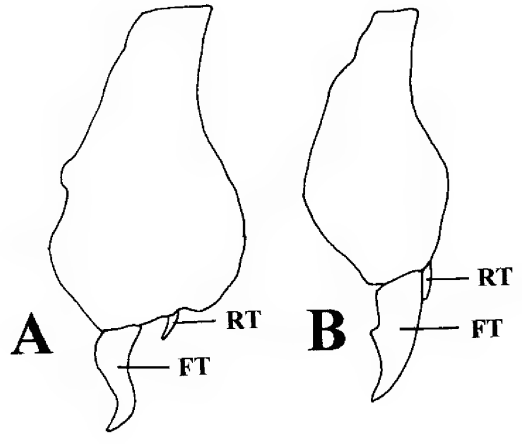


Fig. 6. *Coryphoblennius galerita*, female, 49.6 mm SL. – *(Upper): A.* Right premaxillary, anterior side; – *B.* dentary, anterior side.

Fig. 7. Median part of left premaxillary with functional tooth and replacement tooth. – *(Lower left)*: A. *Coryphoblennius galerita* (male, 61.5 mm SL, Spain, Torremolinos); – B. *Parablennius pilicornis* (female, 75.8 mm SL, France, Hendaye).

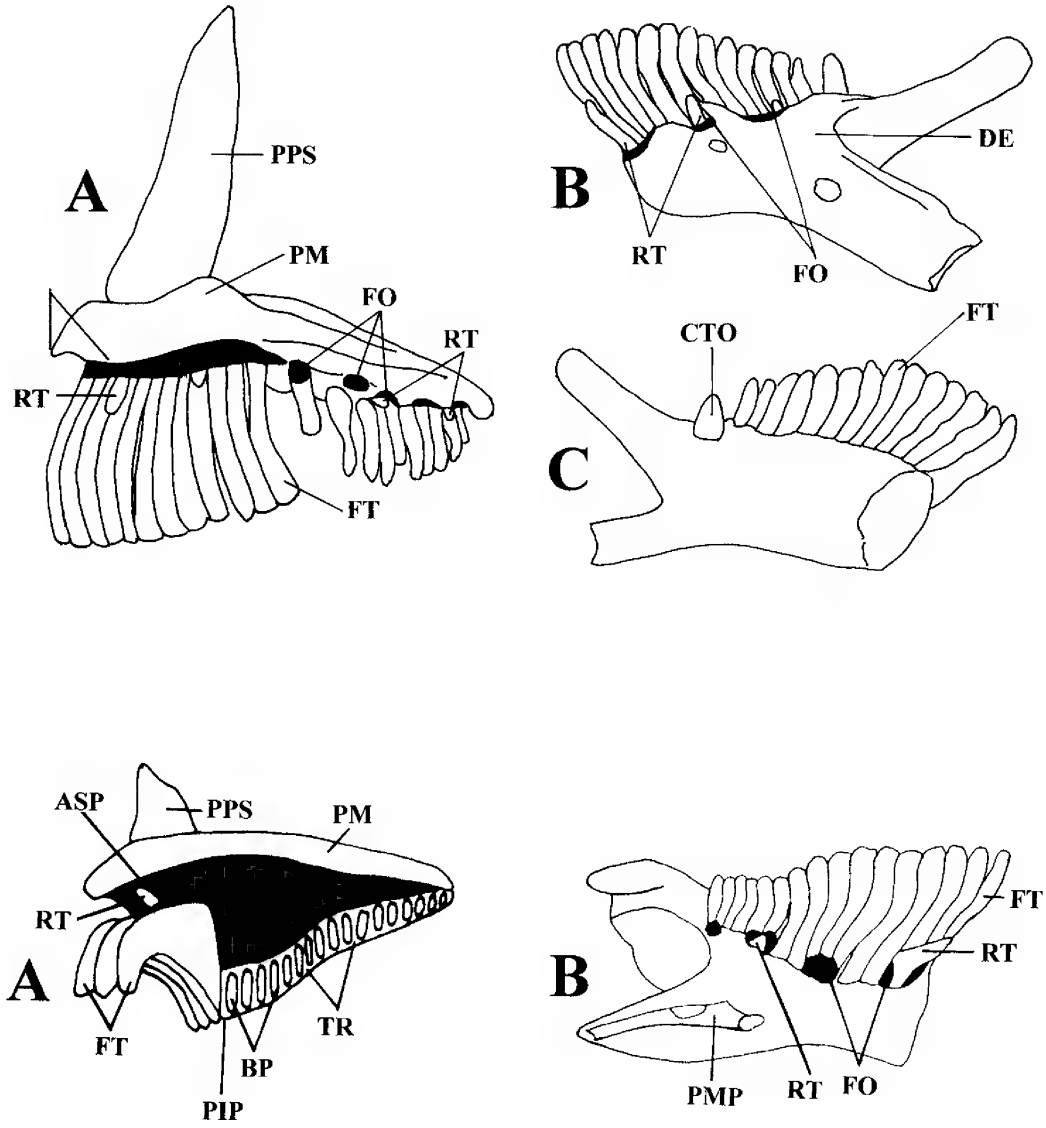


Fig. 8. *Hirculops cornifer,* male, 48.0 mm SL. – *(Upper): A.* Left premaxillary, anterior-inferior side; – *B.* left dentary, anterior side; – *C.* left dentary, posterior side.

Fig. 9. *Antennablennius hypenetes,* male, 49.2 mm SL. – *(Lower): A.* Left premaxillary, anterior-lateral view, functional and replacement teeth mostly removed; – *B.* right dentary, anterior side.

ted directly anterior to the bases of the functional teeth. The bony, closed, median walls of the dentaries of either side are interconnected by a syndesmosis (Fig. 9 B). The canine teeth have their own foramina in the jaw bones; as functional teeth, they are ancylosed with the jaw bones (as in other species and genera).

Mimoblennius atrocinctus has shell-like premaxillaries. The median shell margins of both premaxillaries are closely adjacent in the posterior-inferior area, while they are further and further apart towards the superior and anterior-inferior areas. The anterior-inferior margin of both premaxillaries is free for its whole length, without contact to functional teeth. The functional teeth are attached to a tooth ridge on the

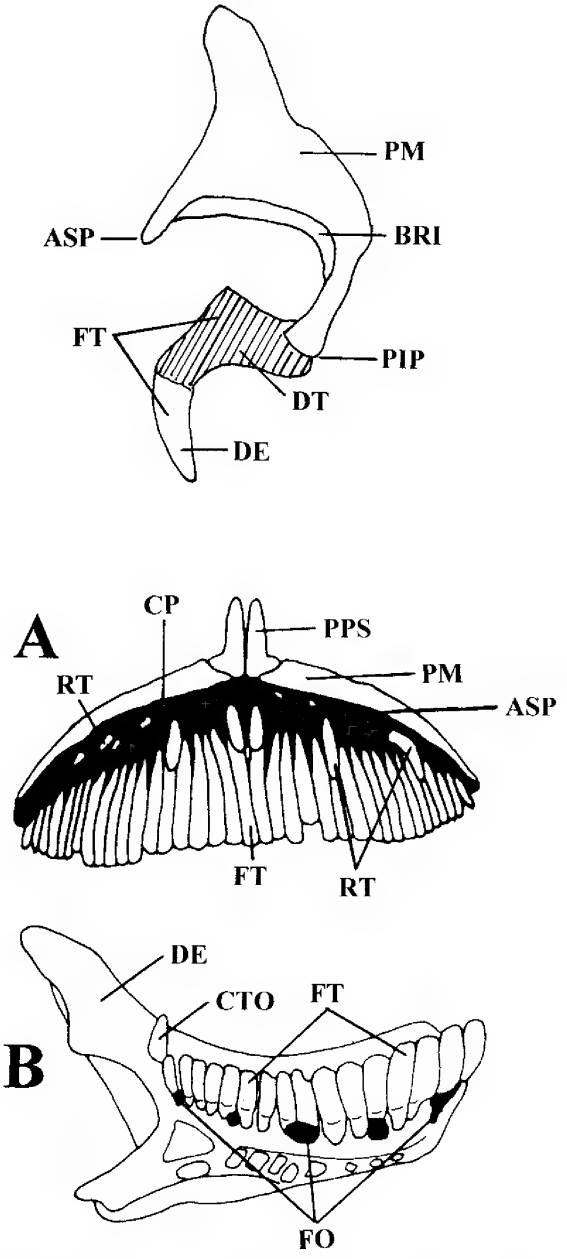
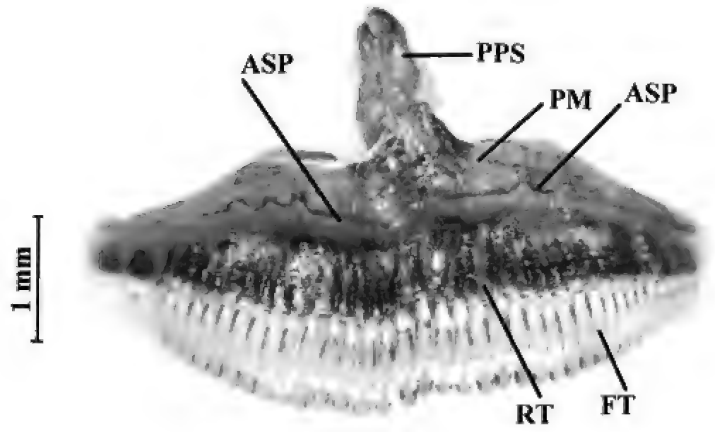


Fig. 10. *Antennablennius hypenetes,* male, 49.2 mm SL. – *(Upper):* Median part of right premaxillary; median wall open except for a small, dorsal bony ridge *(BRI).*
Fig. 11. *Mimoblennius atrocinctus,* male, 33.2 mm SL. – *(Central): A.* Premaxillary, anterior side; – *B.* right dentary, anterior side.

posterior-inferior shell margins of the premaxillaries. The replacement teeth are formed by tissue that is situated within the bony shells; only when they become functional teeth, do they come in contact, through connective tissue, with the bony tooth ridge (Fig. 11 A). The dentaries each consist of a closed bony capsule. Their functional teeth, which are incisiform, are attached to a tooth ridge in the superior sections of the bones. The basal half, which is connected with the tooth ridge, consists of den-



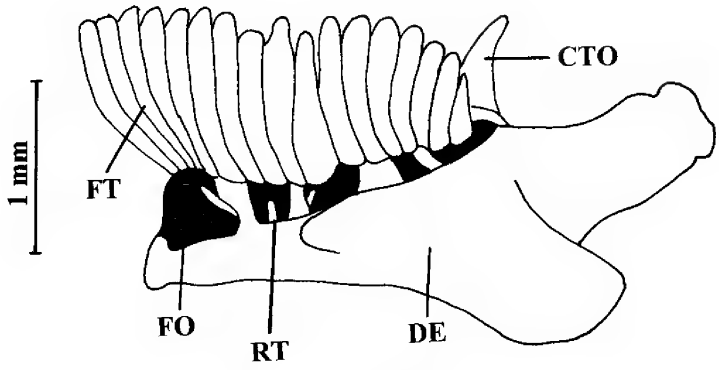


Fig. 12. *Rhabdoblennius ellipes*, female, 50,4 mm SL. – (Upper): Premaxillary, anterior side.
Fig. 13. *Rhabdoblennius ellipes*, female, 50,4 mm SL. – (Lower): Left dentary, anterior side.

tine, the distal half, of dental enamel (Figs 2, 5). Close to the bases of the functional teeth, five foramina for replacement teeth are situated in the bony wall of adult specimens (Fig. 11 B).

Rhabdoblennius ellipes has premaxillaries that form an incomplete bony shell. The anterior-superior margin is freely, roof-like protruding (Fig. 12). The posterior-inferior margin forms the base of the functional teeth; the teeth are attached to the bone by connective tissue. The dentaries form an incomplete bony capsule. In the specimen examined, the anterior-inferior margin is connected with the posterior-superior by four narrow bony bridges. In between these bridges, large foramina for the emission of replacement teeth are found. On either side the median foramina are the largest; they are interconnected in the middle. The bases of the functional teeth are situated on the dentary; they are still incisiform, and attached to the posterior-superior margin by connective tissue (Fig. 13). Species of the genus *Rhabdoblennius* have 44–50 upper jaw teeth, 28–38 lower jaw teeth, a medium-sized posterior canine tooth in the lower jaw, and vomerine teeth.

Teeth of Group 3a: *Nannosalarias nativitatis* (with less than 65 teeth in the lower jaw) has premaxillaries and dentaries forming an incomplete shell. The anterior-

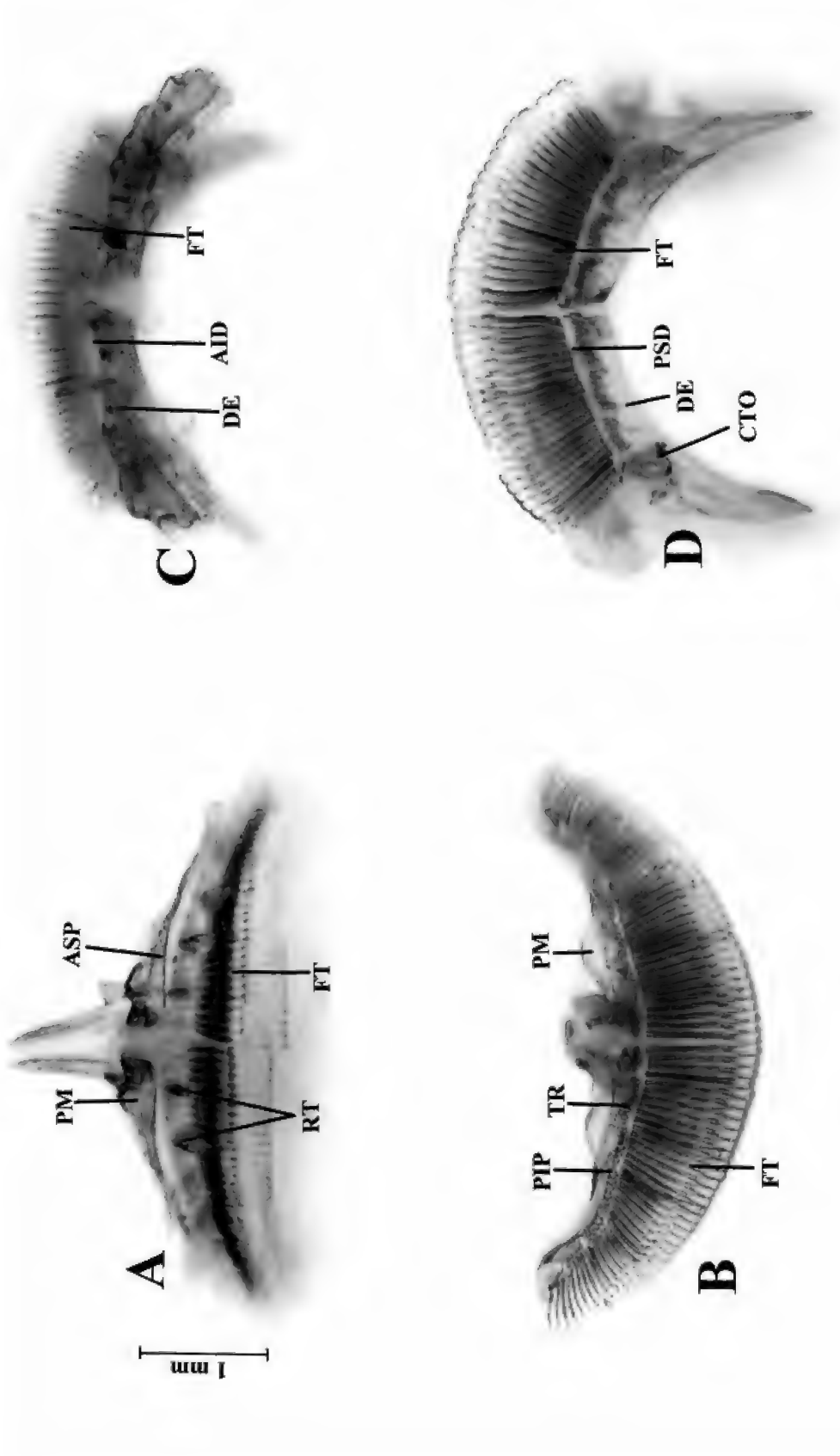


Fig. 14. *Nannosalarias nativitatis*, male, 28.3 mm SL.– *A*. Premaxillaries, anterior side; – *B*. premaxillaries, inferior side; – *C*. dentaries, anterior side; – *D*. dentaries, superior side.

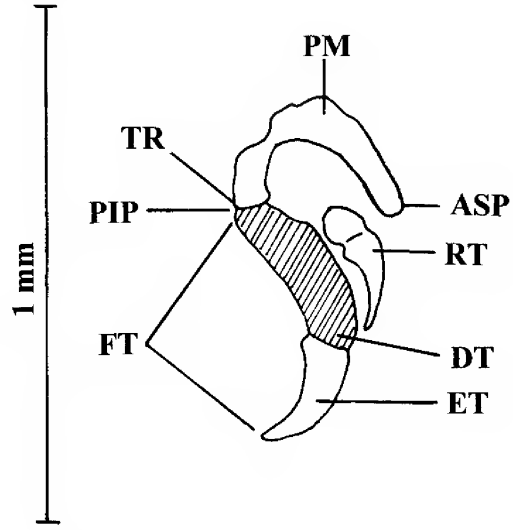


Fig. 15. *Nannosalarias nativitatis,* male, 28.3 mm SL. – Cross-section through the median part of the left premaxillary (schematic). – *Abbreviations:* see chapter 2.1.

superior margin of the premaxillaries and the anterior-inferior margin of the dentaries are free over their whole width, forming the anterior margin of the jaw bones. The functional teeth are not attached to a band of connective tissue, but directly to teeth ridges of the posterior-inferior margin of the premaxillaries and the posterior-superior margin of the dentaries (Figs 14 A–D, 15). The replacement teeth are surrounded by connective tissue and tooth-generating tissue of the bony excavation; they are not in direct contact to the bone. The close contact of the teeth with the jaw margins decreases the mobility of the teeth (less than in species of Group 4). However, the tooth bases are narrow, and mostly rounded (Figs 2, 7). *Nannosalarias* has medium-sized, posterior canine teeth in the lower jaw, and vomerine teeth.

Dodekablennos fraseri has jaws and dentition that are nearly identical with those of *N. nativitatis.* Premaxillaries and dentaries form an incomplete shell. The anterior-superior margin of the premaxillaries and the anterior-inferior margin of the dentaries are free over their whole width. The functional teeth are directly attached to tooth ridges on the posterior-inferior margin of the premaxillaries and the posterior-superior margin of the dentaries. The species has 55–63 upper jaw teeth, 44–47 lower jaw teeth, a medium-sized, posterior canine tooth in the lower jaw, and vomerine teeth (Fig. 16 A–C).

Teeth of Group 3b: In *Ecsenius bicolor,* the bases of all lower jaw functional teeth are not in direct contact with the dentary but adjoined to the its posterior-superior margin by connective tissue. The bases of two-thirds of the functional teeth are attached to the posterior-inferior margin of the premaxillary. The bases of the remaining one-third are attached laterally to connective tissue, without direct contact to bone (Fig. 18). The anterior-superior margin of the premaxillaries and the anterior-inferior margin of the dentaries are roof-like, protruding for their entire width, forming the anterior margin of the jaw bones. On both sides of the dentaries, an anterior and posterior canine tooth is present. This is a unique character of the genus *Ecsenius* (Smith-Vaniz & Springer, 1971; Springer, 1988). The anterior canine

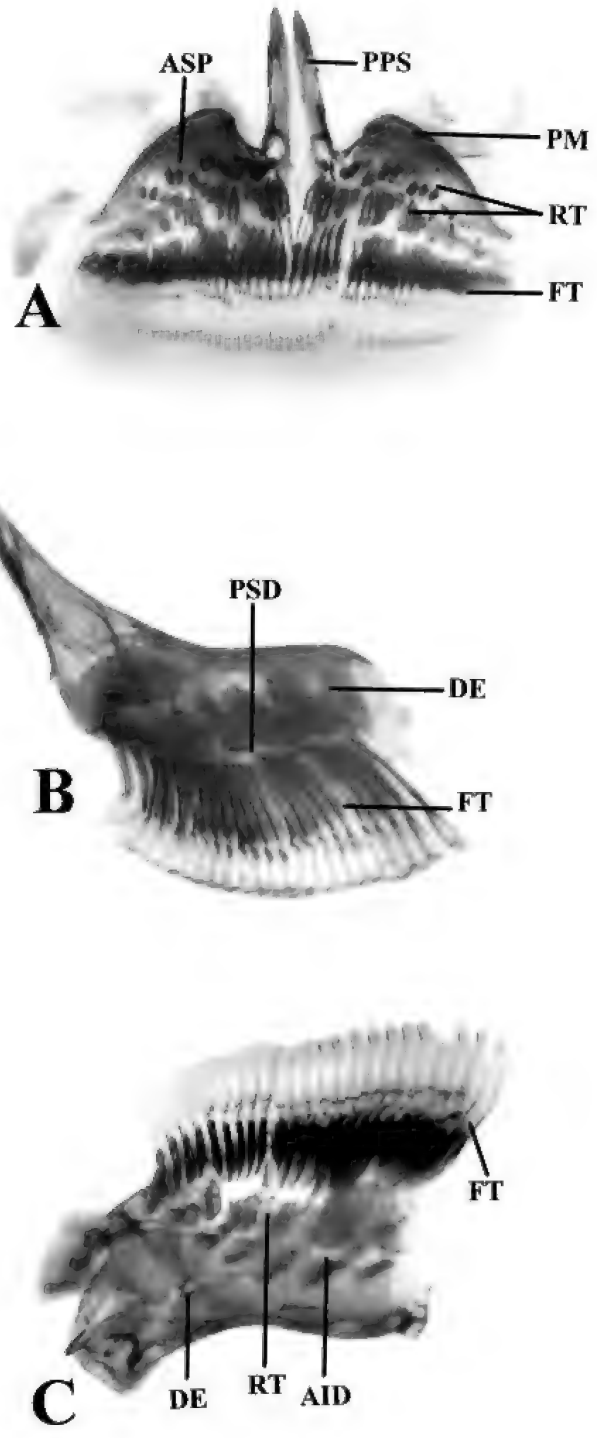


Fig. 16. *Dodekablennos fraseri*, female, 29.3 mm SL. – *A.* Premaxillaries, anterior side; – *B.* right dentary, superior side; – *C.* right dentary, anterior side.

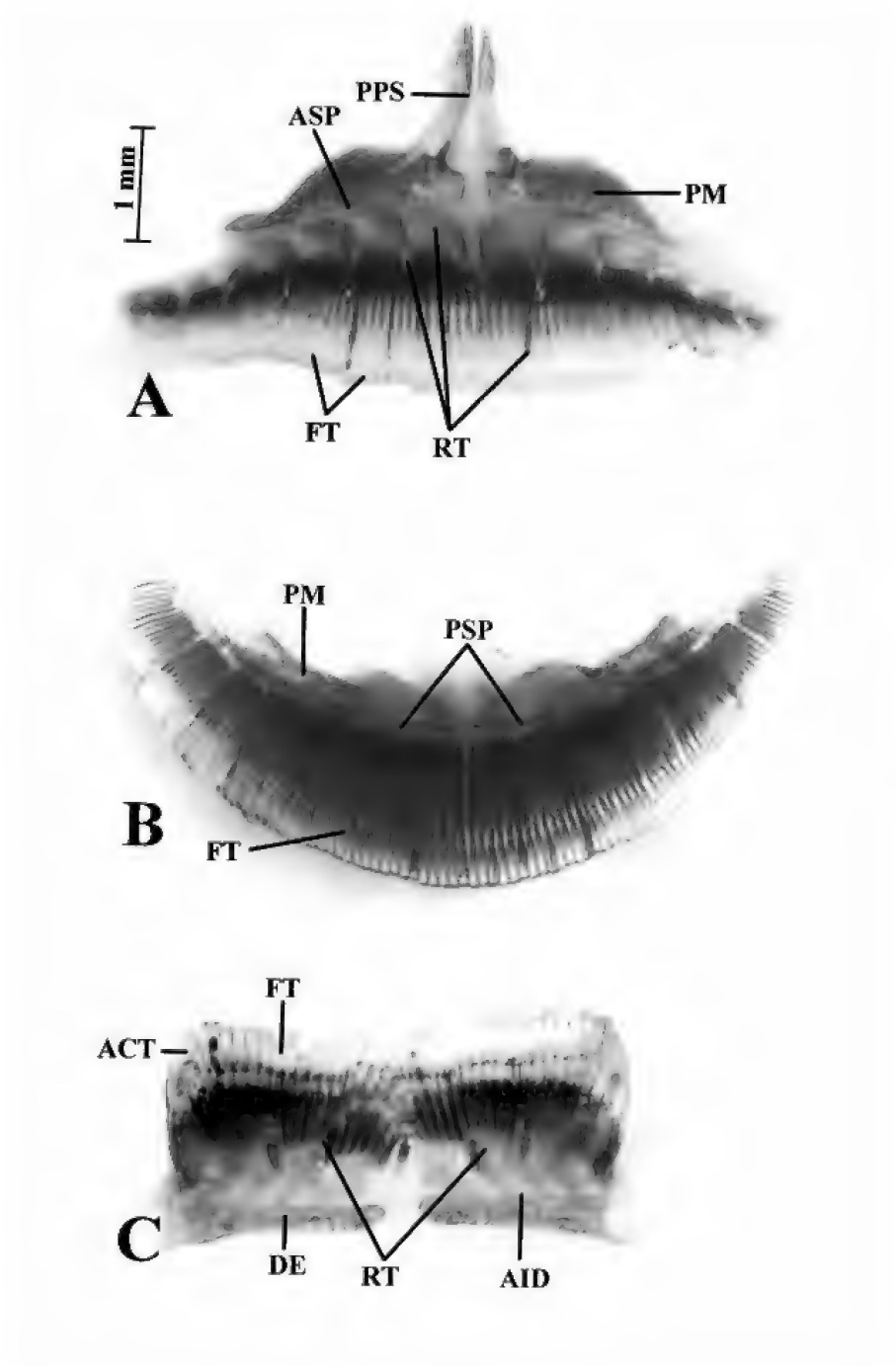


Fig. 17. *Ecsenius bicolor,* male, 47.0 mm SL. – *A.* Premaxillaries, anterior side; – *B.* premaxillaries, inferior side; – *C.* dentaries, anterior side.

tooth is adjacent to the incisors, and its base extends well posterior to the level of the bases of the incisors; the anterior canine tooth is especially separate from the dentary bone. The posterior canine tooth is basally ankylosed to the *processus ascendens* of the dentary.

Teeth of Group 4: In the evolution of a comblike dentition with shell-like premaxillaries and dentaries, and without direct attachment of the functional teeth to the jaw bones, the bases of the functional teeth are connected with the posterior-inferior margin of the premaxillary and the posterior-superior margin of the dentary by tight membranous tissue with bony inlays. Some of these bony inlays are configured narrow, thin, band-like, others are irregular and of different sizes. Near the bases of the functional teeth, small rod-like bony particles are found, which may be adjoined to bony particles in the connective tissue. The bony inlays are apparently remains of a lost direct bony connection between the posterior-inferior margin of the premaxillary and the posterior-superior margin of the dentary. The posterior-inferior margin of the premaxillary and the posterior-superior margin of the dentary often lack a sharp contour. The distance between the premaxillaries and dentaries of either side is more or less vast.

In species possessing incisors, the jaw bones are tightly adjoined by connective tissue. The more comb-tooth character the dentition has, the larger is the distance between the jaw bones.

Exallias brevis also has a narrow distance between the bases of the functional teeth and the posterior-superior margin of the dentaries (Fig. 19 A). The connective tissue between the tooth bases and the dentary margin contains a longitudinal row of small, irregular shaped bony particles (Fig. 20). The anterior-inferior margin of the dentaries is free, with a sharp contour (Fig. 19 B). While the upper jaw teeth are of a comblike type, the functional teeth in the lower jaw are typical incisiform, with a broad, straight tooth base (Figs 2: 4 A–B).

Entomacrodus vermiculatus has the anterior-superior margin of the premaxillary and the anterior-inferior margin of the dentaries free, protruding roof-like, with a sharp contour (Fig. 21). The posterior-inferior margin of the premaxillary and the posterior-superior margin of the dentaries are lacking a sharp contour, forming a firm membrane that is connected with the bases of the functional teeth (Fig. 22). Within that membrane, irregular shaped and sized bony inlays and rodlet-like bony particles are arranged in a row, having contact with the bases of the functional teeth. In the lateral one-fourth of the functional teeth, the membrane is gradually thinning. Here, the bony inlays are mostly lacking, and very few rodlet-like bony particles are found (Figs 23 A–B, 24).

Similar character states are found in the other examined species with a comblike dentition. The bases of the functional teeth are always connected with the posterior-inferior margin of the premaxillaries and the posterior-superior margins of the dentaries by a tight membranous tissue with small bony inlays forming an indirect bony connection (Figs 25 A–B, 26, 27 A–D, 28, 29). Only the anterior margins of the jaw bones are lacking contact with the bases of the functional teeth. In different species, the irregularly configurated bony inlays are of different numbers and sizes.

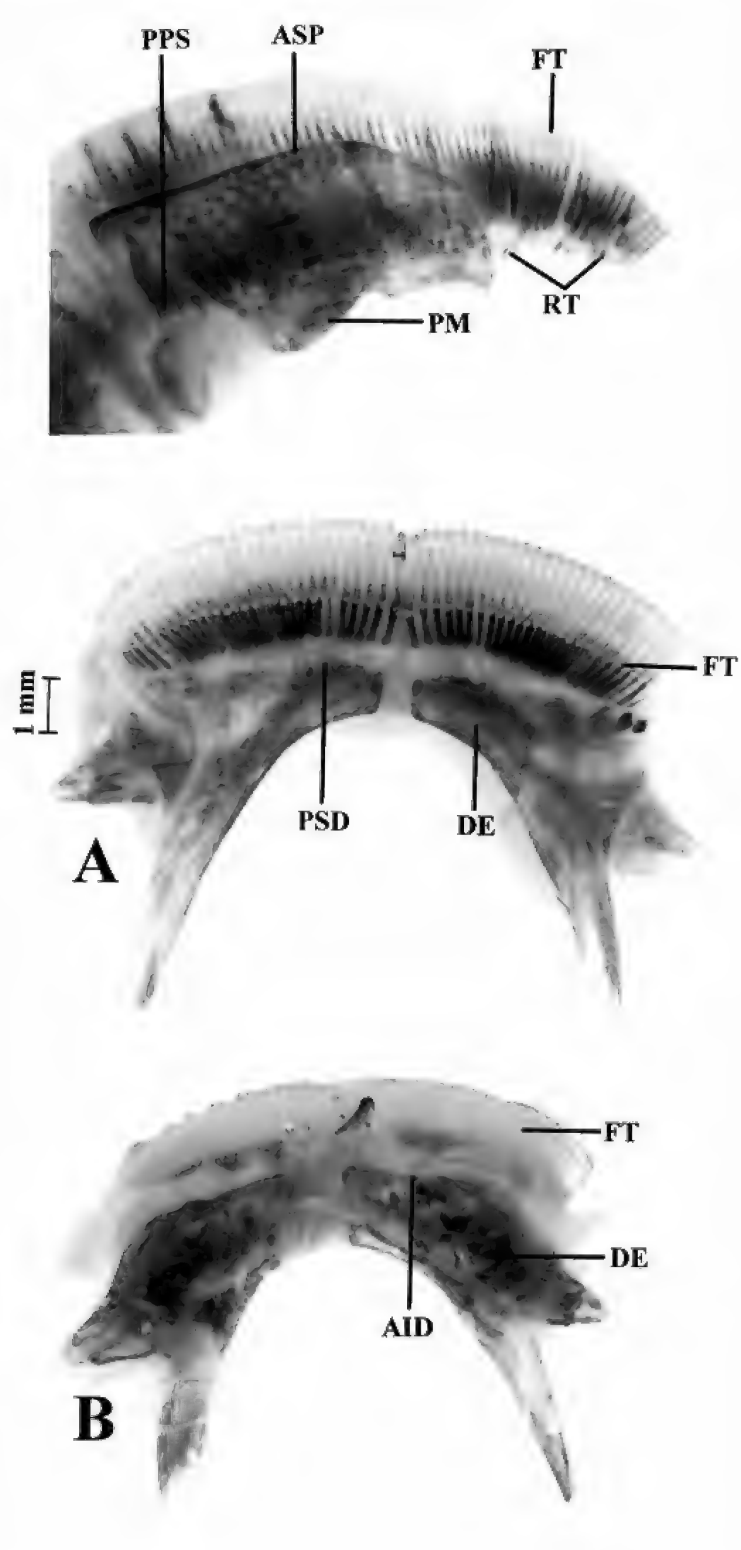
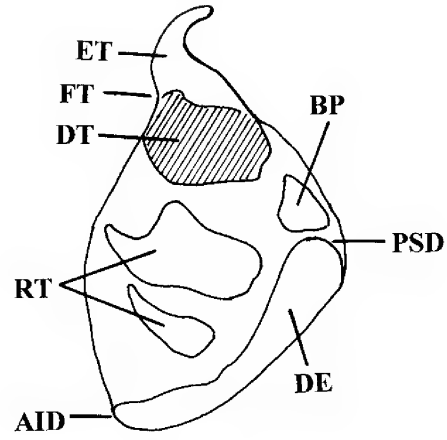
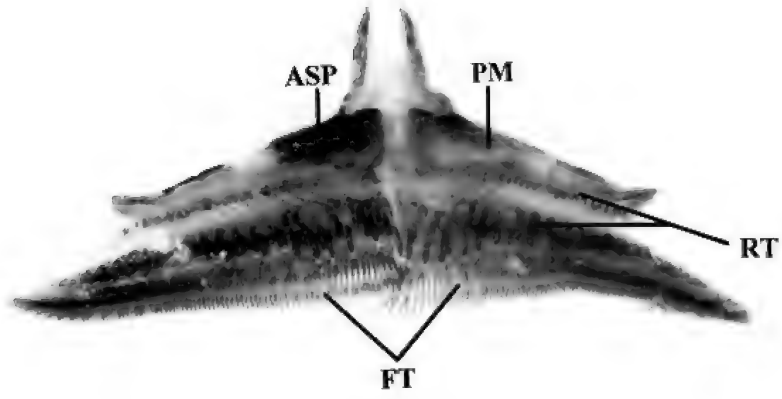


Fig. 18. *Ecsenius bicolor,* male, 47.0 mm SL. – *(Upper):* Right premaxillary, superior side.
Fig. 19. *Exallias brevis,* male, 77.8 mm SL. – *A.* Dentaries, superior side; – *B.* dentaries, inferior side.





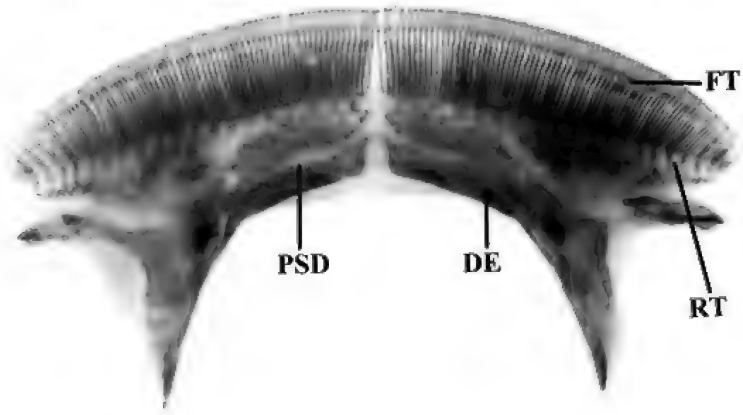
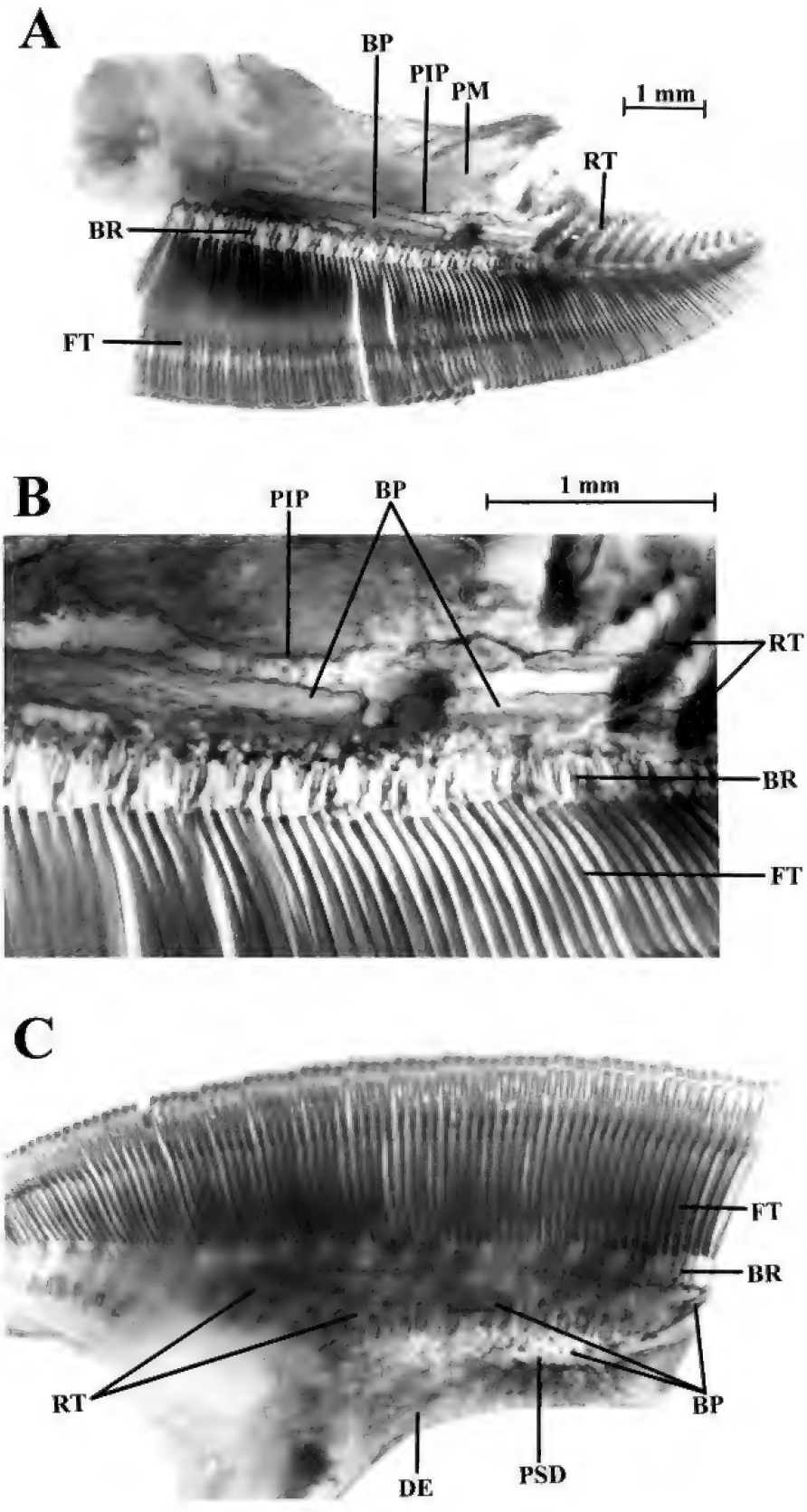


Fig. 20. *Exallias brevis,* male, 77.8 mm SL, Taiwan, Lanyu. – *(Upper):* Right dentary, median cross-section (schematic). Irregular particles of bony tissue *(BP)* in the connective tissue between the bases of the functional teeth and the superior-posterior margin of the dentary.

Fig. 21. *Entomacrodus vermiculatus,* female, 84.3 mm SL. – *(Central):* Premaxillaries, anterior side.

Fig. 22. *Entomacrodus vermiculatus,* female, 84.3 mm SL. – *(Lower):* Dentaries, superior side.


A
BP
PIP
PM
1 mm
RT
BR
FT
B
PIP
BP
1 mm
RT
BR
FT
C
FT
BR
RT
BP
DE
PSD

5. Additional osteological characters

Searching for characters that might distinguish the Parablenniinae and Salariinae, numerous additional anatomical characters were compared. Characters of the neurocranium and viscerocranium, the shape and arragement of bones in the shoulder girdle, the vertebral column, the fins and the lateral line organ were examined.

The anatomy of blenniid skulls was examined by SPRINGER (1968) and BATH (1996). Both authors found numerous variations in the configurations and position of skull bones, but not a single feature characteristic for either the Parablenniinae or the Salariinae. Two character states were treated as synapomorphies by WILLIAMS (1990), supporting the monophyly of the former tribe Parablenniini (Parablenniinae). One of these characters is the configuration of the basibranchial I, that was supposed to be generally straight in the Salariinae but U-shaped in the Parablenniinae. However, in both groups, straight, U-shaped and intermediate configurations of this bone are found (Fig. 30: 1–17). Even within a single genus (e. p. *Hypsoblennius*), all types are found (BATH, 2000a).

The second character assumed to be characteristic for either tribe is epibranchial IV. WILLIAMS (1990) found in species of the Salariini (Salariinae) a simple or paired, bony projection of the median shaft, while the Parablenniini (Parablenniinae) only had a narrow, wing-like protuberance on the posterior margin of the lateral half of the bone. However, wing-like bony protuberances in the lateral section of epibranchial IV, as well as simple or paired projections of the median shaft, are directed dorsally when seen from the front. The wing-like protuberances have quite different configurations; occasionally, they are as wide as or even wider than the bony shaft (Fig. 31: 5–8). The bony wings often have laterally or centrally rounded or pointed corners. The numerous intermediate states of the epibranchial IV (Fig. 31) indicate that this character ist not at all useful to distinguish the Parablenniinae and Salariinae.

A comparison of the circumorbitals shows that their configuration depends on the position and pore number of the bony channel of the infraorbital part of the orbital channel, without anatomical characters that might be useful to distinguish species or genera (Fig. 32: 1–10). The same variation is found in the types of configuration of the infrapharyngobranchial plate and the ceratobranchial V (Fig. 33: 1–6).

SPRINGER (1968) published a detailed examination and discussion of characters in the shoulder girdle of perciform (especially blenniid) fishes. Like former authors, he formally characterized the shoulder girdle by the position and relationships of the radials with the scapula and coracoid. Considering which of the proximal articula-

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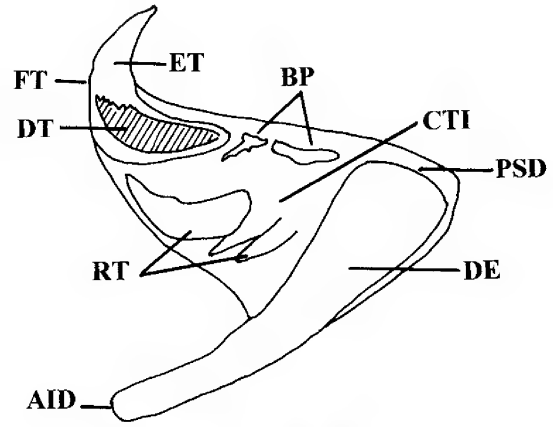
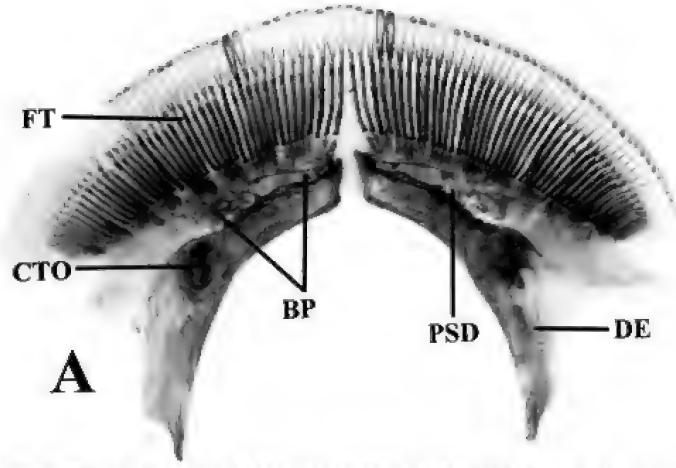
Fig. 23. *Entomacrodus vermiculatus,* female, 84.3 mm SL. – *A.* Right premaxillary, posterior side. Replacement teeth mostly removed. View towards the connective tissue membrane between the bases of the functional teeth and the posterior-inferior margin of the premaxillary. Bony particles in the connective tissue membrane partially shell-like. – *B.* Right premaxillary, posterior side (enlarged section of Fig. 23 A). Shell-like bony particles and rodlets in the connective tissue membrane between the bases of the functional teeth and the posterior-inferior margin of the premaxillary. – *C.* Left dentary, superior side. – *Explanations: BP* irregular sized and shaped bony particles in the connective tissue between the posterior-superior margin of the dentary and the bases of the functional teeth; *BR* rodlet-like bony particle at the base of the functional teeth.





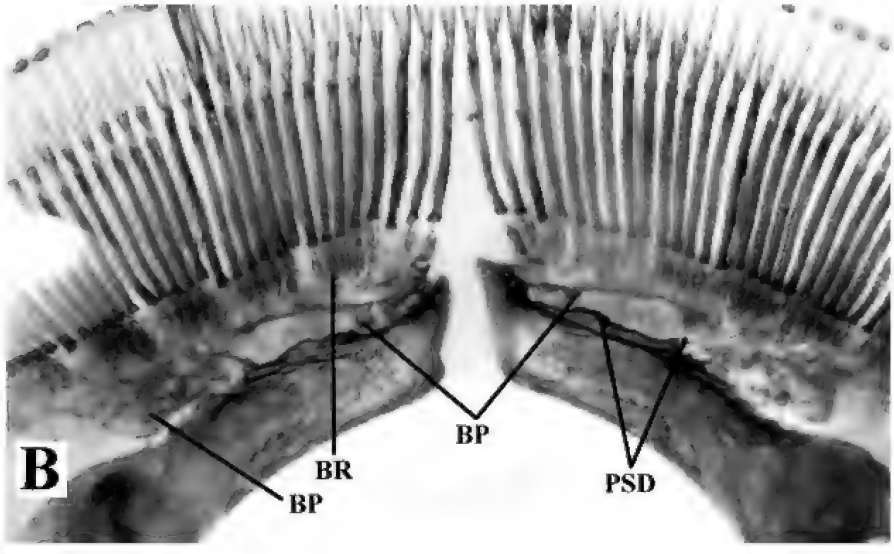


Fig. 24. *Entomacrodus vermiculatus*, female, 84.3 mm SL. – *(Upper):* Right dentary, median cross-section (schematic). *BP* irregular sized and shaped bony particles in the connective tissue between the posterior-superior margin of the dentary and the base of the functional teeth.

Fig. 25. *Blenniella cyanostigma*, male, 50.7 mm SL. – *A.* Dentaries, superior side; – *B.* median parts of the dentaries, superior side; *BP* bony particles.

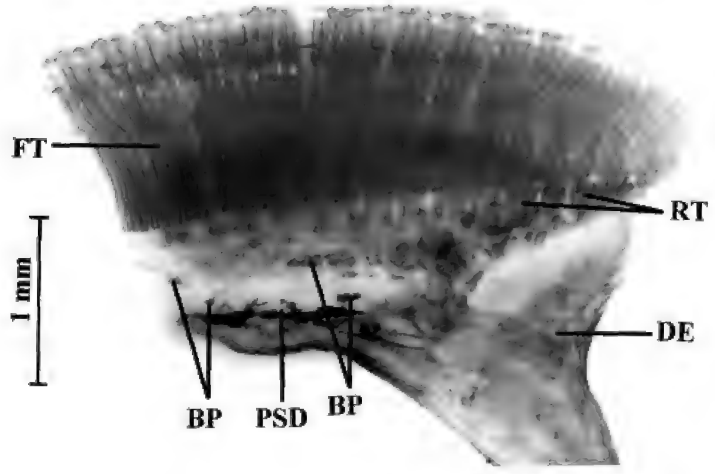


Fig. 26. *Istiblennius lineatus,* male, 83.0 mm SL. – Right dentary, superior side.

tions of the radials I–IV were dorsally and ventrally in contact with the scapula, with the interstice between scapula and coracoid, or with the coracoid, he recognized the formulae 3–1–0, 3–0–1, 2–1–1, 2–0–2, 1–1–2 and 1–0–3. However, these formulae are insufficient to characterize the shoulder girdle, as additional characters need to be considered; therefore, I reexamined the shoulder girdle of blenniid fishes (Fig. 34: 1). In order to demonstrate the relationships between the bases of the radials and the posterior margins of scapula and coracoid as well as their interstice, two formulae were added. The new set of shoulder girdle formulae is characterized as follows:

I Formula 3–1–0: Proximal bases of radials I, II and III are attached to the posterior margin of the scapula. Proximal base of radial IV is attached to the interstice between scapula and coracoid (Fig. 34: 2);

II Formula 3–0–1: Proximal bases of radials I, II and III are attached to the posterior margin of the scapula. Proximal base of radial IV is attached to the posterior margin of the coracoid (Fig. 34: 3);

III Formula 2–1a–1: Proximal bases of radials I and II are attached to the posterior margin of the scapula. More than 60 % of the proximal base of radial III is attached to the posterior margin of the scapula and to the interstice between scapula and coracoid; less than 40 % of its proximal base are reaching the posterior margin of the coracoid (Fig. 34: 4);

IV Formula 2–1–1: Proximal base of radial III attached to interstice between scapula and coracoid, and (in equal parts) to the posterior margins of scapula and coracoid *(Omobranchus punctatus);*

V Formula 2–1b–1: Proximal bases of radials I and II are attached to the posterior monotypy of the scapula. More than 60 % of the proximal base of radial III are attached to the posterior margin of the coracoid and the interstice between scapula and characteristic; less than 40 % are attached to the posterior margin of the scapula (Fig. 34: 5–6);

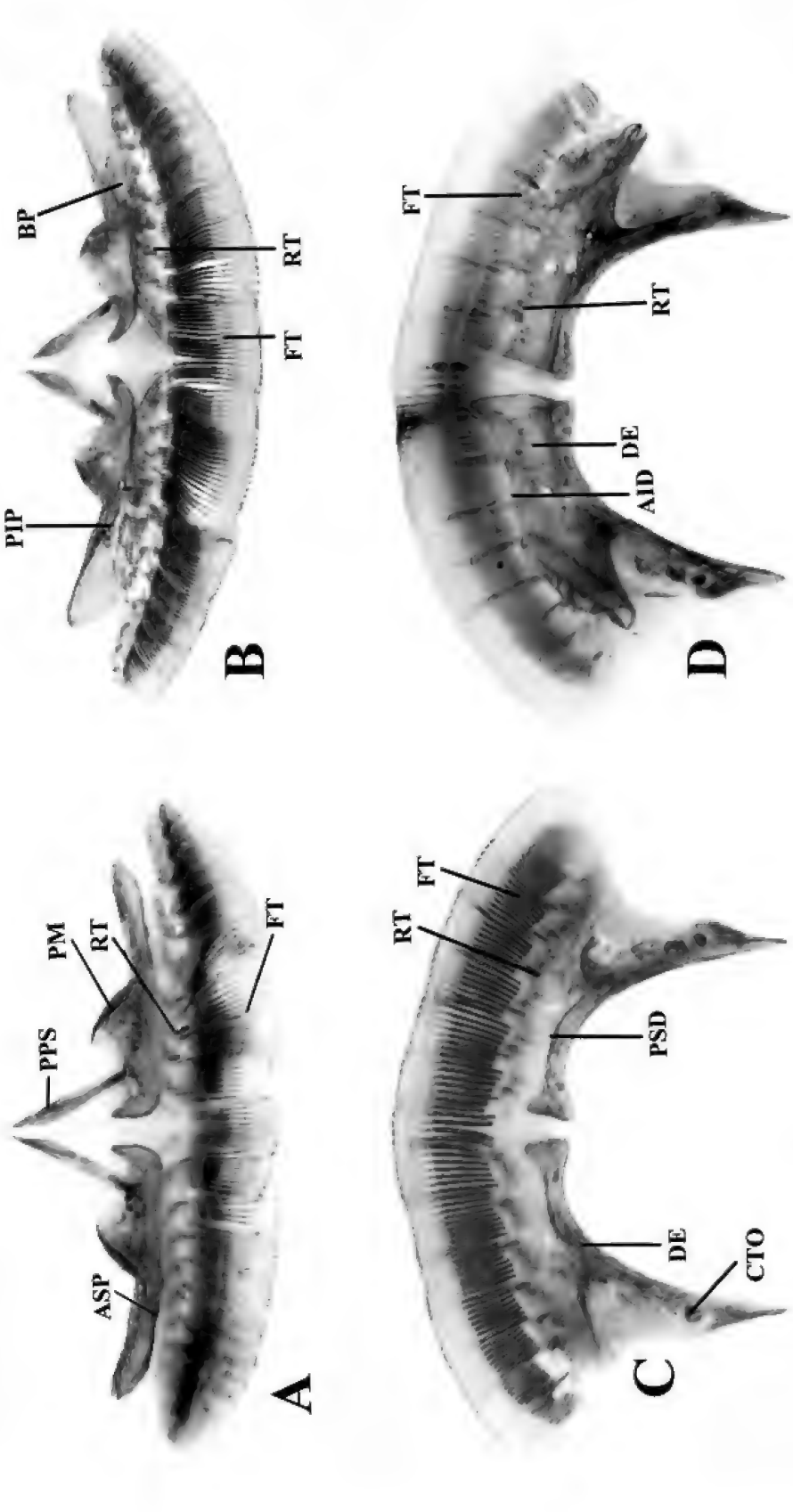


Fig. 27. *Salarias fasciatus*, male, 41.0 mm SL. – *A.* Premaxillaries, anterior side; – *B.* premaxillaries, posterior side; – *C.* dentaries, superior side; – *D.* dentaries, inferior side.

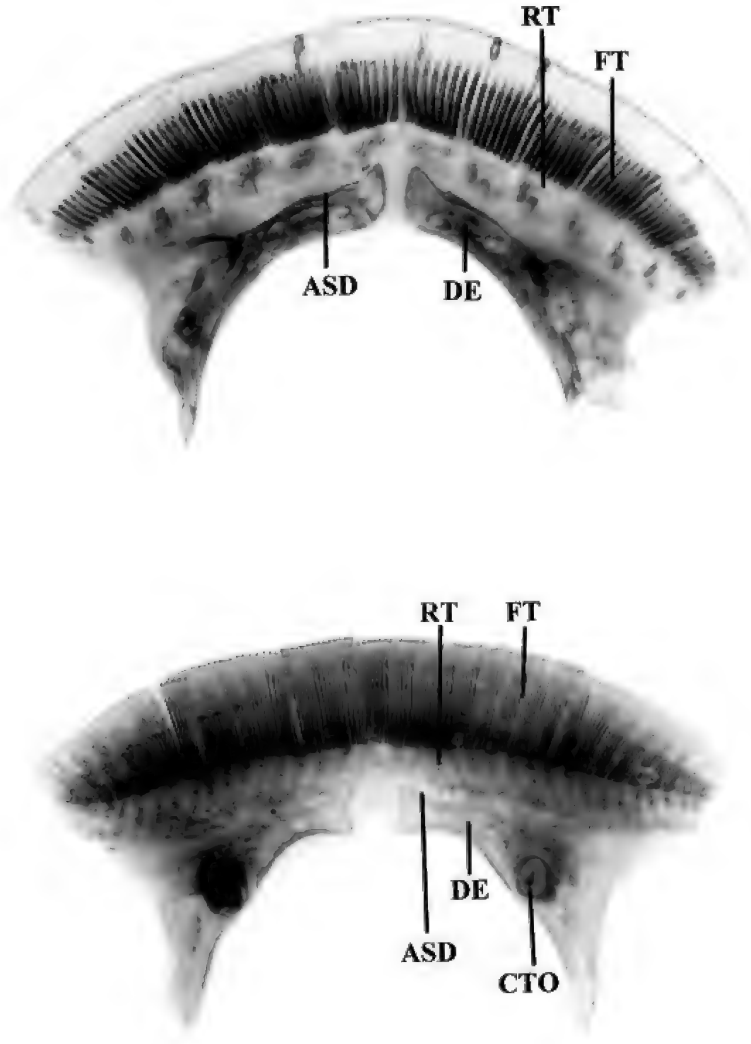


Fig. 28. *Salarias sinuosus,* male, 33.6 mm SL. – *(Upper):* Dentaries, superior side.
Fig. 29. *Praealticus tanegasimae,* male, 87.6 mm SL. – *(Lower):* Dentaries, superior side.

VI Formula 2–0–2: Proximal bases of radials I and II are attached to the posterior margin of the scapula. Proximal bases of radials III and IV attached to the posterior margin of the coracoid (Fig. 34: 7–10);

VII Formula 1–1–2: Proximal base of radial I attached to the posterior margin of the scapula. Radial II covers the interstice between scapula and coracoid. Proximal bases of radials III and IV attached to the posterior margin of the coracoid (Fig. 34: 11);

VIII Formula 1–0–3: Proximal base of radial I attached to the posterior margin of the scapula. Proximal bases of radials II, III and IV attached to the posterior margin of the coracoid *(Plagiotremus azaleus).*

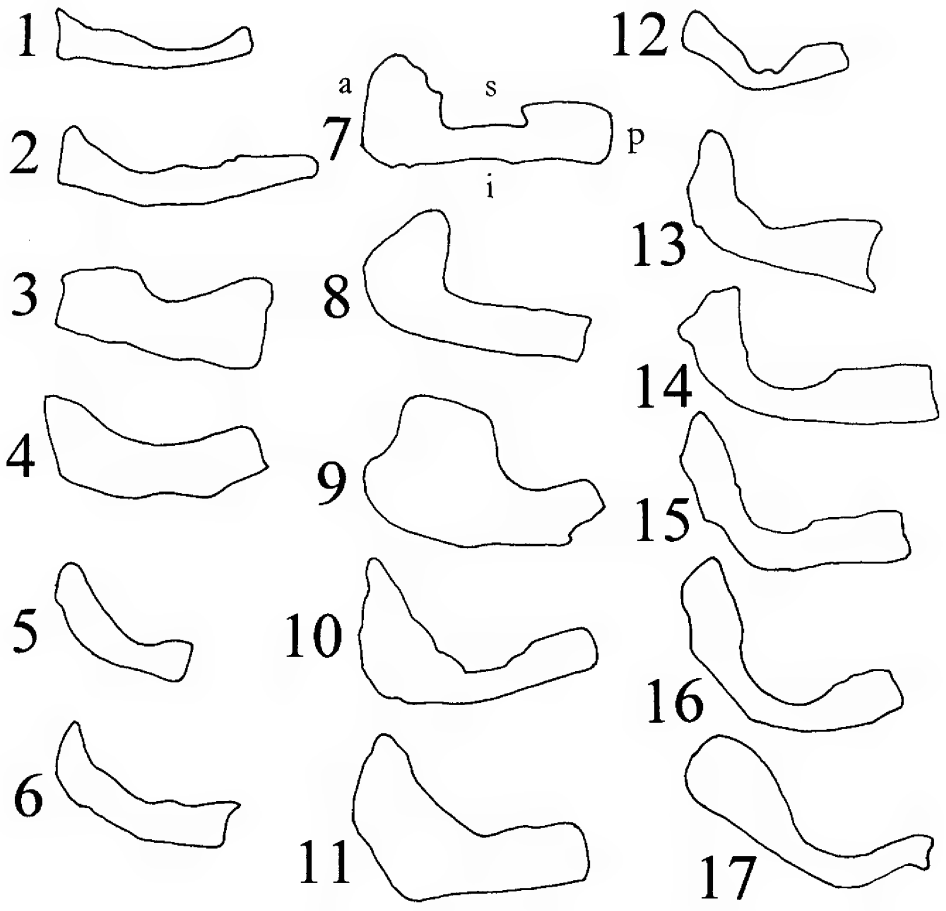


Fig. 30. Basibranchial I in blenniid fish species of the groups Parablenniini and Salariini. – *Abbreviations: a* anterior side; *i* inferior side; *p* posterior side; *s* superior side.
1. *Hypsoblennius gilberti;* – 2. *H. gentilis;* – 3. *Exallias brevis;* – 4. *Cirrisalarias bunares;* – 5. *Dodekablennos fraseri;* – 6. *Parablennius gattorugine;* – 7. *Salaria fluviatilis;* – 8. *Blenniella cyanostigma;* – 9. *Istiblennius lineatus;* – 10. *Hypleurochilus bananensis;* – 11. *Parablennius sanguinolentus;* – 12. *Hypsoblennius proteus;* – 13. *Antennablennius hypenetes;* – 14. *Parablennius tentacularis;* – 15. *Scartella cristata;* – 16. *Hypsoblennius jenkinsi;* – 17. *H. striatus.*

The results for 59 species of Blennidae and 1 species of Carangidae (as outgroup) are compared in Tab. 3. A nearly complete overlap is evident for the groups Parablenniinae and Salariinae; the radial formulae are therefore not useful to distinguish the two groups (BATH, 2000b).

Additional characters of the shoulder girdle, like open or closed shape of the scapula, size of the interstice between the base of scapula and coracoid, bony protuberances at the bases of radials I and II, are likewise useful to distinguish species or genera but neither characteristic for the Parablenniinae nor for the Salariinae.

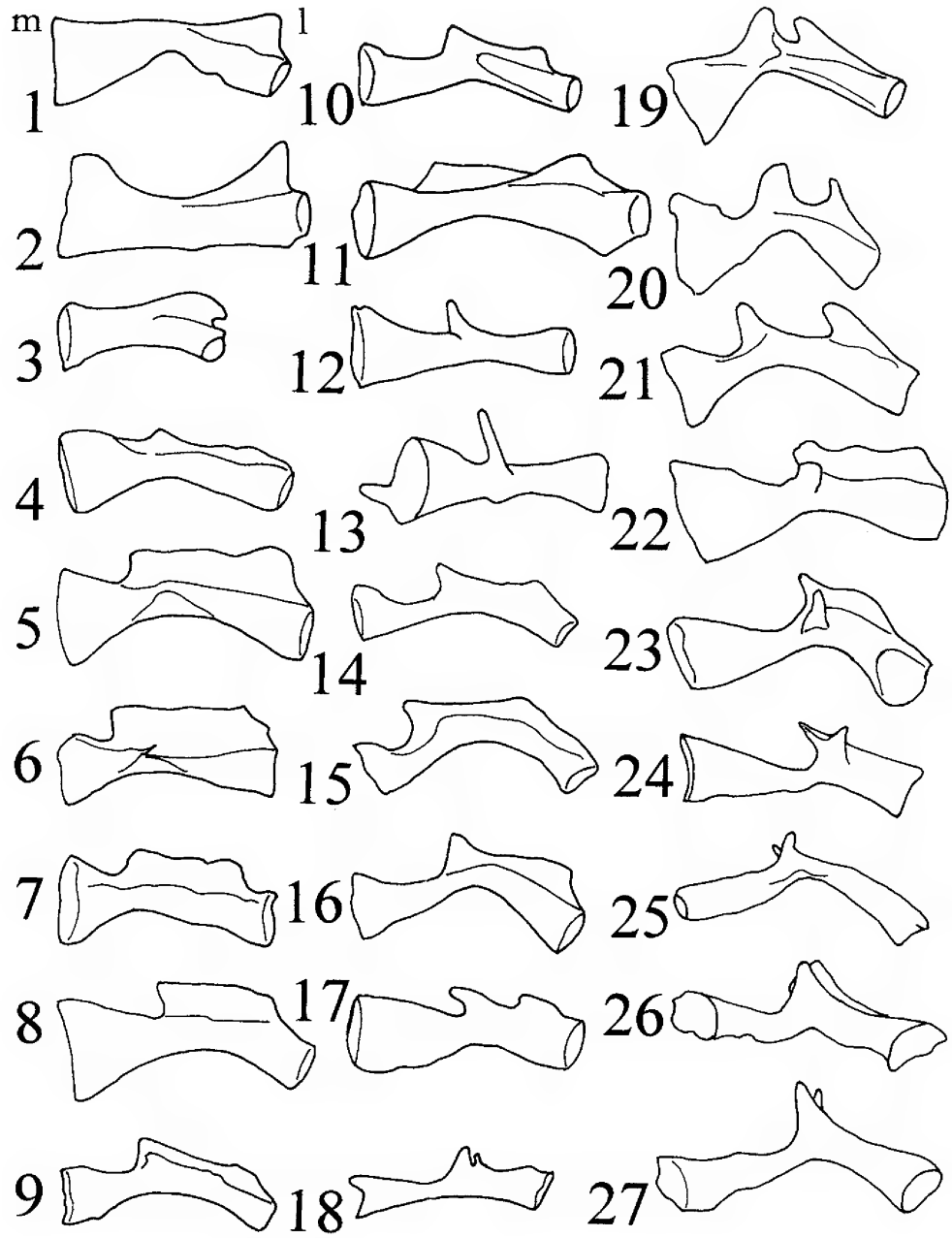


Fig. 31. Epibranchial IV in blenniid fish genera of the groups Parablenniini and Salariini. – *Abbreviations: l* lateral; *m* median. – 1. *Hypsoblennius gentilis;* – 2. *H. paytensis;* – 3. *H. brevipinnis;* – 4. *Paralipophrys trigloides;* – 5. *Hypleurochilus bananensis;* – 6. *Scartella cristata;* – 7. *Salaria fluviatilis;* – 8. *Parablennius pilicornis;* – 9. *P. sanguinolentus;* – 10. *P. gattorugine;* – 11. *Aidablennius sphynx;* – 12. *Nannosalarias nativitatis;* – 13. *Istiblennius lineatus;* – 14. *Hypsoblennius striatus;* – 15. *Lipophrys canevae;* – 16. *Dodekablennos fraseri;* – 17. *Cirrisalarias bunares;* – 18. *Ecsenius bicolor;* – 19. *Rhabdoblennius ellipes;* – 20. *Antennablennius hypenetes;* – 21. *Mimoblennius atrocinctus;* – 22. *Hirculops cornifer;* – 23. *Entomacrodus vermiculatus;* – 24. *Blenniella cyanostigma;* – 25. *Exallias brevis;* – 26. *Istiblennius rivulatus;* – 27. *I. edentulus.*

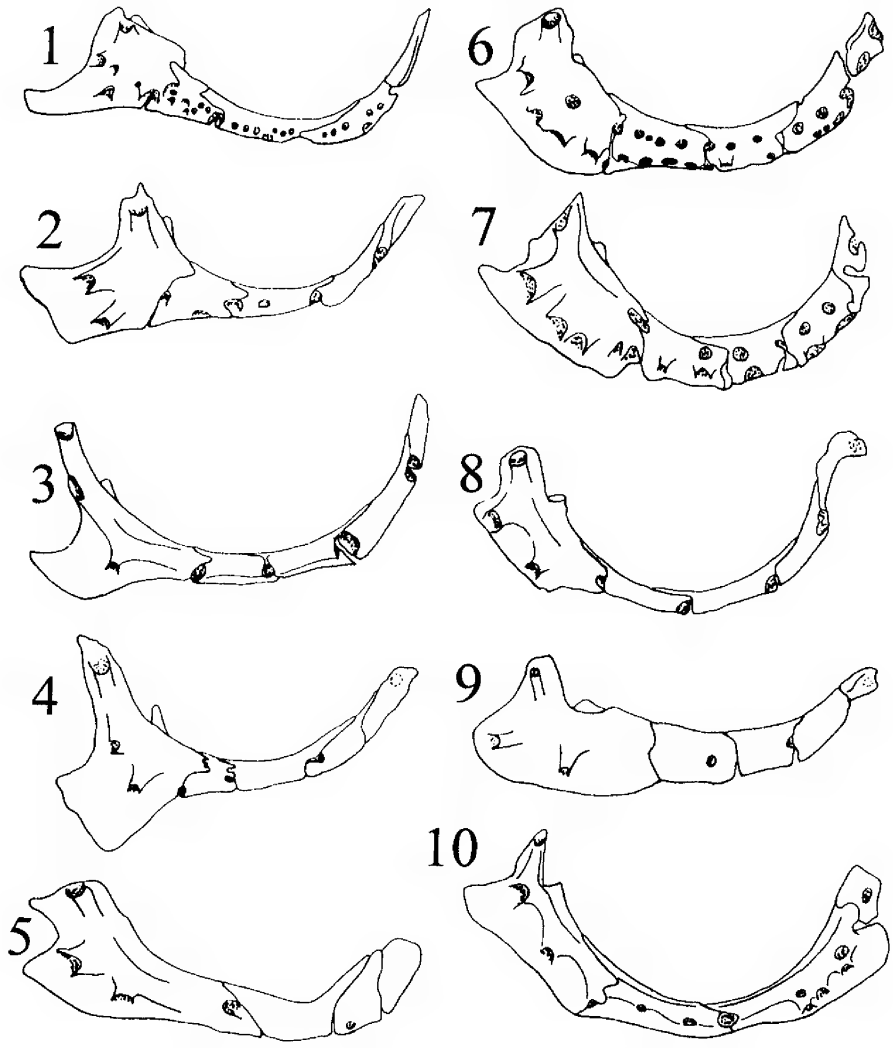


Fig. 32. Circumorbitals I–V in blenniid fishes; left side of head. – 1. *Exallias brevis;* – 2. *Entomacrodus vermiculatus;* – 3. *Salarias fasciatus;* – 4. *Istiblennius lineatus;* – 5. *Cirrisalarias bunares;* – 6. *Parablennius pilicornis;* – 7. *Hypsoblennius brevipinnis;* – 8. *Chasmodes saburrae;* – 9. *Lipophrys canevae;* – 10. *Hypsoblennius exstochilus.*

Tab. 3. Radial formulae of 59 species of the family Blenniidae and 1 species of the family Carangidae (used as outgroup). – *Explanations: m* is the number of species assigned to each formula; *n* is the total number of species of each taxon examined; radial formulae I–VIII are explained on p. 31 ff.

Taxon/group	n	Radial formula (m)							
		I	II	III	IV	V	VI	VII	VIII
Blenniidae:									
Parablenniini	39	–	2	6	3	17	11	–	–
Salariini	16	–	–	–	–	1	14	–	1
Omobranchini	2	–	–	–	1	–	–	1	–
Nemophini	2	–	–	–	–	–	–	1	1
Carangidae:									
Hemicaranx leucurus	1	1	–	–	–	–	–	–	–

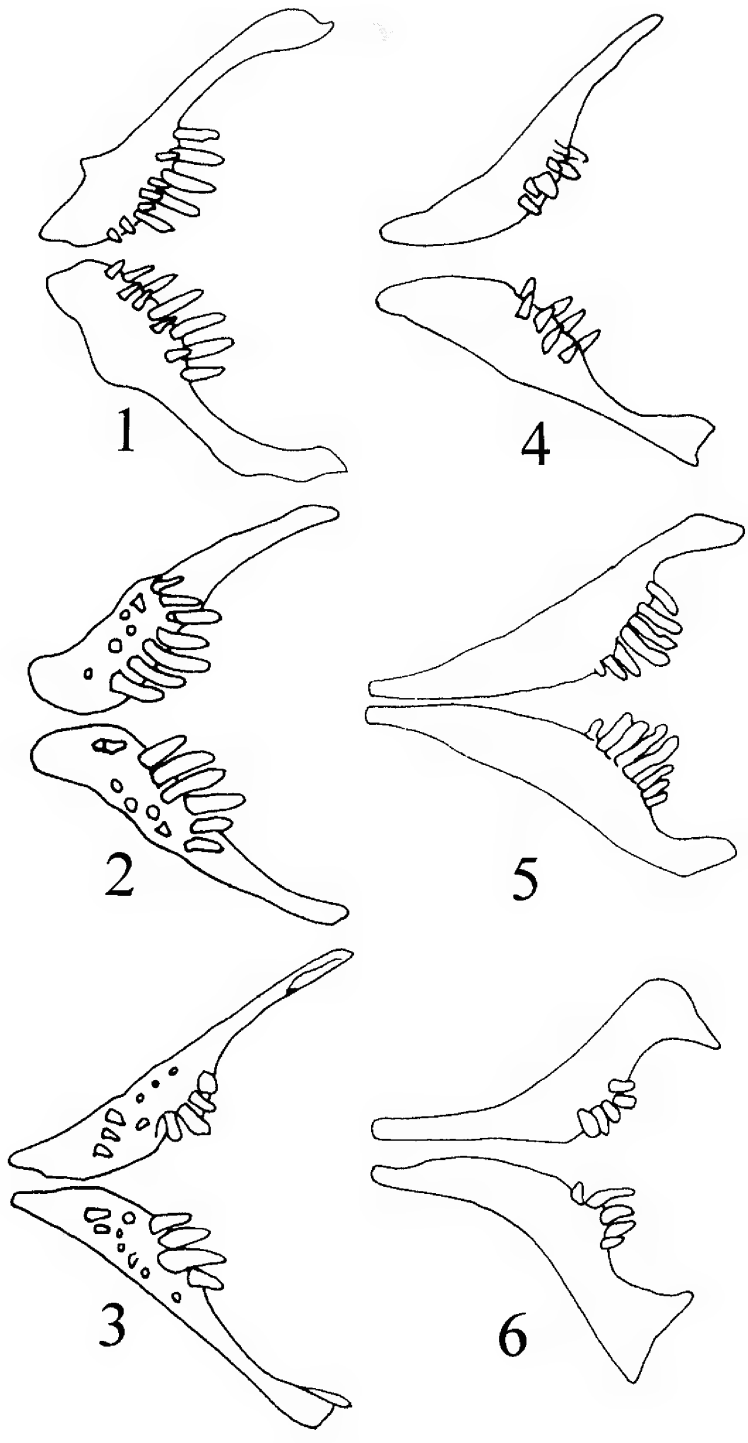


Fig. 33. Ceratobranchial V in blenniid fish genera of the groups Parablenniini and Salariini; superior side. – 1. *Parablennius pilicornis;* – 2. *Hirculops cornifer;* – 2. *Coryphoblennius galerita;* – 4. *Dodekablennos fraseri;* – 5. *Salarias fasciatus;* – 6. *Blenniella cyanostigma.*

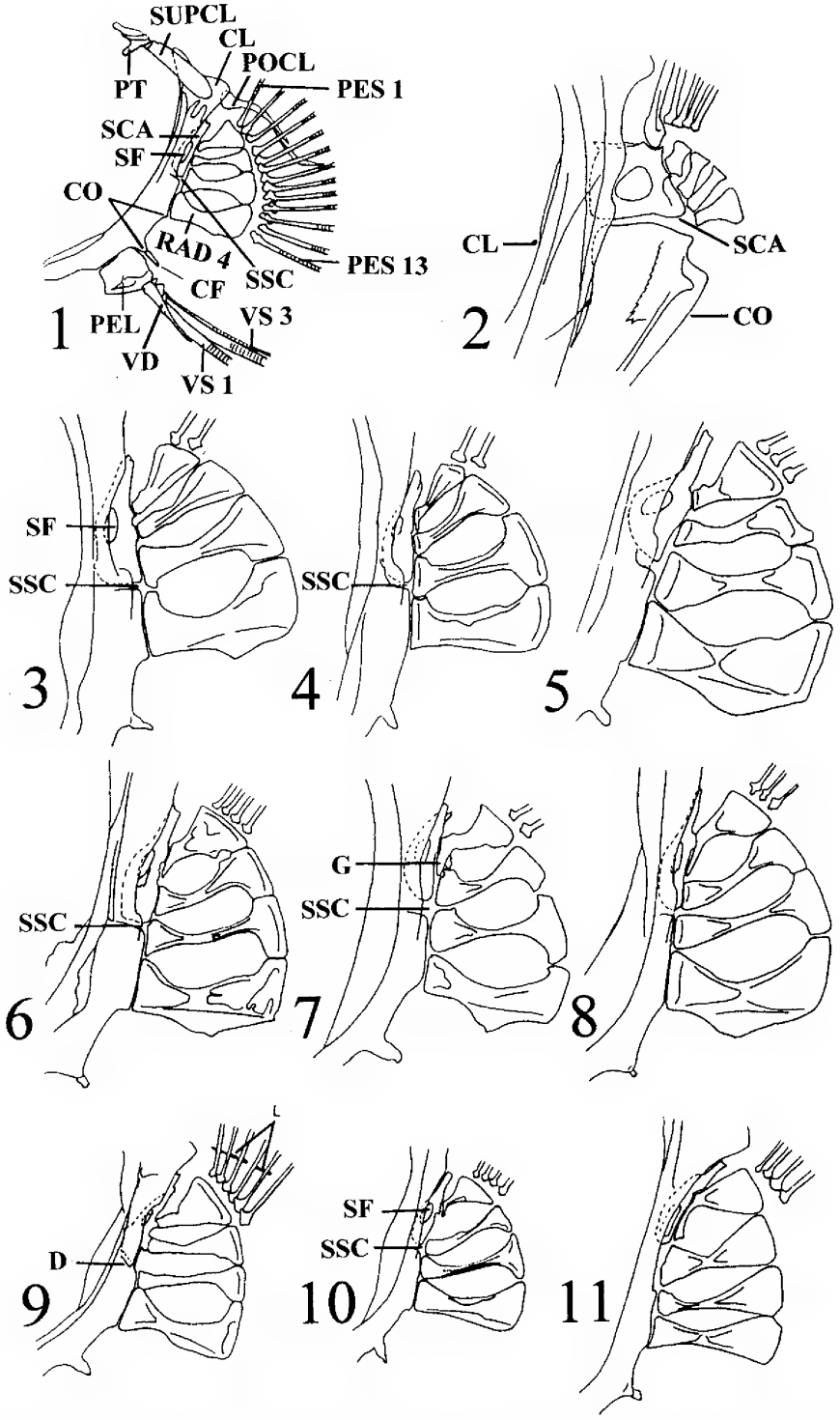


Fig. 34. 1. Blenniid shoulder girdle bones (schematic). – 2.–11. examples for the position of radial bases relative to scapula and coracoid. – 2. *Hemicaranx leucurus;* – 3. *Lipophrys canevae;* – 4. *L. dalmatinus;* – 5. *Hypsoblennius gilberti;* – 6. *Parablennius incognitus;* – 7. *Chasmodes saburrae;* – 8. *Parablennius goreensis;* – 9. *Praealticus tanegasimae;* – 10. *Salarias fasciatus;* – 11. *Enchelyurus petersi.* – *Abbreviations: CF* extension of coracoid; *CL* cleithrum; *CO* coracoid; *D* indentation between scapula and coracoid; *PEL* pelvic; *PES* pectoral rays; *POCL* postcleithrum; *RAD* radials; *SCA* scapula; *SF* scapular foramen; *SSC* interstice between scapula base and coracoid; *SUPCL* supracleithrum; *VD* unsegmented pelvic fin ray; *VS* segmented pelvic fin rays.

6. Lateral line system

No differences could be found in the head and body lateral line systems of the Parablenniinae and Salariinae. Both groups include species and genera with a nearly constant number of dermal pores in the head lateral line system. These species always have low pore numbers (e.g. 44 in *Cirrisalarias bunares,* 54 in *Hypsoblennius striatus*). If the dermal pore number is constant, this is also true for the number of pores in the bony lateral canals. If the pore numbers are higher, they are not constant; then the canals leading from the bony pores to the dermal pores are branched. The larger the number of dermal pores in a species, the higher is its range of variation: the number of pores usually increases with body size.

Within several genera, great differences in the pore numbers of the species may be observed. *Cirripectes castaneus* has 96 dermal head pores, and *C. vanderbilti* has 1397 pores; *Hypsoblennius striatus* has 54 dermal pores, and *H. paytensis* has 815 pores.

The number of dermal pores of the lateral line system is only useful to distinguish species, not genera or suprageneric groups.

7. Discussion

While the former tribes Parablenniini and Salariini are clearly distinguished from the tribes Blenniini, Omobranchini, Parablenniinae and Nemophini, and the latter 4 tribes are separated from each other by constant synapomorphic characters (Smith-Vaniz, 1976), not a single character was found that distinguished the Parablenniini from the Salariini.

The previously assumed differences in the dentition of the Parablenniini and Salariini are rejected because of the presence of intermediates between incisiform and comb-like dentition in several genera; it is therefore impossible to clearly distinguish and support the monopyly of either group.

On the basis of the results of the above examination of different species and genera of the two groups, there is a clear evolutionary trend to develop a comblike dentition out of an incisiform dentition; the presence of a comblike dentition is considered to be apomorphic. Of course, the intermediate forms are usually not closely related.

Several anatomical characters show a trend of developing a comblike dentition, starting with modifications of the premaxillary. Although the premaxillary of a taxon may have typical comblike teeth and a shell-like structure, the dentary teeth of the same taxon have incisiform teeth with firm contact with the posterior-superior margin.

Several forms which are intermediate between an incisiform dentition and a comblike dentition have been observed. In the most primitive intermediate form, the premaxillaries and dentaries form a closed bony capsule. However, the replacement tooth foramina are enlarged. The bony bridges between the foramina are narrower, and some of them are gradually lost. The premaxillary margin is more or less ridge-like or bulb-like protruding over the foramina. The functional teeth are barely mobile; they are attached to the jaw bones (e.g. in *Cirrisalarias, Coryphoblennius*).

Another intermediate form has a premaxillary that opens shell-like in its median-

anterior section. The anterior-superior margin is freely protruding. The lateral parts of the premaxillaries are closed, forming a bony cavity. The median functional teeth are situated on the posterior-inferior margin of the shell-like section, while the lateral teeth are positioned on the ventral side of the closed section of the premaxillary. The replacement teeth are either emitted freely, or laterally (like the functional teeth) through bony foramina (e. g. in *Hirculops*).

In the next step towards a comblike dentition, the premaxillaries form an incomplete shell, with the anterior-superior margin protruding roof-like on its whole width. The functional teeth are attached to tooth ridges of the inferior-posterior margin of the premaxillaries. The dentaries from a closed capsule with a tooth ridge for the functional teeth, and with foramina for the replacement teeth (e. g. *Antennablennius, Mimoblennius, Rhabdoblennius*).

In *Nannosalaris, Dodekablennos* and *Ecsenius bicolor,* the dentaries and premaxillaries form an incomplete shell. The anterior-superior margin of the premaxillaries and the anterior-inferior margin of the dentaries protrude freely, roof-like. The functional teeth are connected with the posterior margins of the jaw bones. This connection is lost by the lateral dentary teeth of *Ecsenius bicolor.*

Some of the species with a comblike dentition have small, irregular bony inlays in the connective tissue between the tooth bases and the superior margin of the dentary. The dentary margin does not have a sharp contour.

A species with a typical comblike dentition has completely lost the connection between the posterior margins of the jaw bones and the bases of the functional teeth. The premaxillary and dentary form complete shells. Bony inlays are absent. The posterior-superior margin of the dentaries has a sharp contour.

The distinction between the former Parablenniini and Salariini is no longer justified. The genera of these two groups should be united in a single group.

Hitherto, the family Blenniidae has been subdivided into several tribes, but not into different subfamilies. This classification is not fully in accordance with the recommended division of the family group (family, subfamily, tribe, etc.; ICZN 1999, Art. 35.1). Usually, if there are tribes, there should be subfamilies first.

The former tribes Parablenniini and Salariini should be united in a subfamily Salariinae (type genus *Salarias* Cuvier, 1817). The other former tribes should be raised to subfamilies as well: the Omobranchini to a subfamily Omobranchinae (type genus *Omobranchus* Ehrenberg in Cuvier & Valenciennes, 1836), the Phenablenniini to a subfamily Phenablenniinae (type genus *Phenablennius* Bleeker, 1859), and the Nemophini to a subfamily Nemophinae (type genus *Nemophis* Kaup, 1858).

The subfamily Salariinae may be divided into 4 groups according to dentition characters:

Group 1: Genera with an incisiform dentition.

Group 2: Genera with a dentition intermediate between incisiform and comblike. Replacement tooth foramina enlarged, with a loss of bony bridges between some foramina. Premaxillaries and dentaries not forming an incomplete shell.

Group 3: Genera with premaxillaries and dentaries forming an incomplete shell. All or most functional teeth of the premaxillaries connected with the posterior-inferior margin. Functional teeth of the dentaries connected with the posterior-superior margin.

Group 4: Genera with premaxillaries and dentaries forming a complete shell. Connective tissue between functional teeth of the premaxillary and posterior-inferior premaxillary margin just like the dentary and posterior-superior margin, either with inlays of irregular bony fragments (in that case premaxillary and dentary margin without sharp contour), or without such inlays (then premaxillary and dentary margin with sharp contour).

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